1

Genetic Resources of Kiwifruit: Domestication and Breeding

*A. Ross Ferguson**
The Horticulture and Food Research Institute of New Zealand Ltd.
Private Bag 92 169, Auckland, New Zealand

*Hongwen Huang***
Wuhan Botanical Garden / Wuhan Institute of Botany
The Chinese Academy of Sciences
Moshan, Wuchang, Wuhan City, Hubei 430074
People's Republic of China

- I. INTRODUCTION
- II. GENETIC DIVERSITY AND GERMPLASM RESOURCES OF *ACTINIDIA*
  - A. Taxonomy, Geographic Distribution, and Evolution
    - 1. The Genus and Infrageneric Subdivisions
    - 2. Geographic Distribution
    - 3. Vertical Distribution
    - 4. Geographic Distribution and Reticulate Evolution
    - 5. The *A. chinensis*/*A. deliciosa* Complex
    - 6. The Problem of *A. rufa*

*I thank R. A. Martin and A. G. Seal for reading parts of the manuscript, F. A. Gunson and I. J. Warrington for editing the entire manuscript, S. Cookson for preparing Fig. 1.1, and B. Shaw and M. Heffer for preparing the plates. The preparation of this review was supported in part by the NZ Foundation for Science Research and Technology C06X0006.

**I thank S. Wang, Z. Jiang, and Z. Zhang for assembling data during the early stage of preparing the manuscript, Z. Li for preparing Table 1.3, many other colleagues for providing data, and many students for their useful contributions to the preparation of the first draft of this manuscript. The preparation of this review was partially supported by NSF of China (30070082) and KIP of CAS (KSCX2-SW-104) and WZ no.051001 of Laboratory of Conservation Genetics, WBG-CAS.

Horticultural Reviews, Volume 33, Edited by Jules Janick
ISBN 978-0-471-73214-3

- B. Variation in Fruit Characteristics
  - 1. Fruit Size
  - 2. Fruit Shape
  - 3. Fruit Hairs and Skin
  - 4. Fruit Color
  - 5. Ripening Indicators
  - 6. Fruit Texture
  - 7. Fruit Flavor
  - 8. Health Constituents
  - 9. Other Fruit Characteristics
- C. Gender Variation
- D. Ploidy Variation
  - 1. Basic Chromosome Number
  - 2. Ploidy Races
  - 3. Nuclear DNA Content and Flow Cytometry
  - 4. Consequences of Ploidy Variation for Kiwifruit Breeding
- E. Molecular Heterozygosity

III. NATURAL DISTRIBUTION OF *ACTINIDIA*
- A. Geographic Distribution of Commercially Important Species
- B. Regional Distribution, Natural Habitats, and Wild Production
  - 1. China
  - 2. Amur Oblast, Khabarovsk Krai, and Primorski Krai, Russian Far East
  - 3. Sakhalin and Kuril Islands
  - 4. Japan
  - 5. Korea
  - 6. Cambodia
  - 7. Laos
  - 8. Vietnam
  - 9. Myanmar (Burma)
  - 10. Thailand
  - 11. Malaysia and Indonesia
  - 12. Northern India

IV. DOMESTICATION AND COMMERCIALIZATION OF KIWIFRUIT
- A. Early Use in China, Japan, and Korea
- B. Early Western Introductions of *Actinidia* Species
- C. Domestication and Commercialization of *A. arguta*, *A. kolomikta*, and *A. polygama*
- D. Domestication and Commercialization of *A. chinensis* and *A. deliciosa*
  - 1. First Botanical Specimens
  - 2. Introduction of *A. deliciosa* into Cultivation
  - 3. Commercialization of *A. deliciosa*
  - 4. Commercialization of *A. chinensis*
- E. The World Kiwifruit Industry
  - 1. World Plantings of Kiwifruit
  - 2. World Production of Kiwifruit
  - 3. Important Cultivars of *A. chinensis* and *A. deliciosa* in International Trade
  - 4. Cultivars of *A. chinensis* and *A. deliciosa* in China
  - 5. Segmentation of the Kiwifruit Market by Fruit Flesh Color

V. ORIGINS OF KIWIFRUIT CULTIVARS
- A. Cultivars of *A. chinensis* and *A. deliciosa*
  - 1. Selection from the Wild

        2. Seedling Selections
        3. Clonal Selections
        4. Budsports or Mutations
        5. Selections from Controlled Crosses
        6. Pollenizer Selections
    B. Cultivars of *A. arguta*, *A. kolomikta*, and *A. rufa*
    C. Interspecific Crosses
VI. FROM GENETIC DIVERSITY TO CULTIVAR DEVELOPMENT
LITERATURE CITED

I. INTRODUCTION

This review describes genetic diversity within the genus *Actinidia* and discusses the processes by which kiwifruit were domesticated, a classic example of the exploitation of wild germplasm resources.

In China the genus *Actinidia* is known by the name, 猕猴桃, or mihoutao [monkey peach]. Throughout the rest of the world, the most commonly used name is kiwifruit. It is important to define how we use the word "kiwifruit" in this review as the meaning has evolved since the name was originally devised for selections of *Actinidia deliciosa*, the first *Actinidia* species to be cultivated commercially as a fruit plant. (A list of the *Actinidia* taxa discussed in this review is given in Table 1.1.) Seed of *A. deliciosa* had been taken from China to New Zealand in 1904 and the very first commercial kiwifruit orchard was in production by about 1930 (Ferguson and Bollard 1990). The name "kiwifruit" was proposed when the fresh fruit were first exported to the United States in 1959. The name was promoted in this and in other developing markets and, within ten years, had become the accepted name for the fruit. It is now generally accepted in scientific, technical, and commercial literature and acceptance of the name was undoubtedly hastened by advertising campaigns promoting the kiwifruit produced in New Zealand. The full name "kiwifruit" should be used, not the shortened version of "kiwi" as this is used in other contexts.

The selection of good cultivars, especially of the cultivar 'Hayward', and the successful export of fresh kiwifruit from New Zealand led to rapid expansion of kiwifruit plantings, first in New Zealand and then throughout the rest of the world. China was stimulated to show a greater interest in its wild resources of kiwifruit and this resulted in the successful domestication and cultivation of a second, closely related *Actinidia* species, *A. chinensis*, which may have even greater commercial potential than *A. deliciosa* itself. Now about one quarter of all kiwifruit plantings in China are of *A. chinensis* and this species is also being increasingly cultivated in other countries; in New Zealand, for example,

Table 1.1. Taxa of *Actinidia* Lindl. mentioned in text or tables. The nomenclature followed is based on Liang (1984).

A. arguta (Sieb. et Zucc.) Planch. ex Miq.
A. arguta var. *cordifolia* (Miq.) Bean
A. arguta var. *giraldii* (Diels) Voroshilov
A. arguta var. *nervosa* C.F.Liang
A. arguta var. *purpurea* (Rehder) C.F.Liang ex Q.Q.Chang
A. arisanensis Hayata
A. callosa Lindl.
A. callosa var. *acuminata* C.F.Liang
A. callosa var. *discolor* C.F.Liang
A. callosa var. *ephippioidea* C.F.Liang
A. callosa var. *formosana* Finet et Gagnep.
A. callosa var. *henryi* Maxim.
A. callosa var. *pubiramula* C.Y.Wu
A. callosa var. *strigillosa* C.F.Liang
A. carnosifolia C.Y.Wu
A. carnosifolia var. *glaucescens* C.F.Liang
A. chengkouensis C.Y.Chang
A. chinensis Planch.
A. chinensis var. *jinggangshanensis* (C.F.Liang) C.F.Liang et A.R.Ferguson
A. chinensis var. *rufopulpa* (C.F.Liang et R.H.Huang) C.F.Liang et A.R.Ferguson
A. chrysantha C.F.Liang
A. cinerascens C.F.Liang
A. cinerascens var. *longipetiolata* C.F.Liang
A. cinerascens var. *tenuifolia* C.F.Liang
A. cylindrica C.F.Liang
A. cylindrica var. *cylindirica* f. *obtusifolia* C.F.Liang
A. cylindrica var. *reticulata* C.F.Liang
A. deliciosa (A.Chev.) C.F.Liang et A.R.Ferguson
A. deliciosa var. *changanensis*—not yet formally described
A. deliciosa var. *chlorocarpa* (C.F.Liang) C.F.Liang et A.R.Ferguson
A. deliciosa var. *coloris* T.H.Lin et X.Y.Xiong
A. deliciosa var. *longipila* (C. F. Liang et R. Z. Wang) C.F.Liang et A.R.Ferguson
A. eriantha Benth.
A. eriantha f. *alba* C.F.Gan
A. eriantha var. *brunnea* C.F.Liang
A. eriantha var. *calvescens* C.F.Liang
A. × *fairchildii* Rehder
A. fanjingshanensis S.D.Shi et Q.B.Wang
A. farinosa C.F.Liang
A. fasiculoides C.F.Liang
A. fasiculoides var. *cuneata* C.F.Liang
A. fasiculoides var. *orbiculata* C.F.Liang
A. fortunati Finet et Gagn.
A. fulvicoma Hance
A. fulvicoma var. *lanata* (Hemsl.) C.F. Liang
A. fulvicoma f. *hirsuta* (Finet et Gagnep.) C.F.Liang
A. fulvicoma var. *pachyphylla* (Dunn) Li
A. gagnepaini Nakai
A. glauco-callosa C.Y.Wu
A. glaucophylla F.Chun
A. glaucophylla var. *asymmetrica* (F.Chun) C.F.Liang
A. glaucophylla var. *robusta* C.F.Liang
A. globosa C.F.Liang
A. gracilis C.F.Liang
A. grandiflora C.F.Liang
A. guilinensis C.F.Liang

A. hemsleyana Dunn
A. hemsleyana var. *kengiana* (Metcalf) C.F.Liang
A. henanensis C.F.Liang
A. henryi Dunn
A. henryi var. *glabricaulis* (C.Y.Wu) C.F.Liang
A. henryi var. *polyodonta* Hand.-Mazz.
A. holotricha Finet et Gagnep.
A. hubeiensis H.M.Sun et R.H.Huang
A. hypoleuca Nakai
A. indochinensis Merr.
A. jiangkouensis S.D.Shi et Z.S.Zhang
A. jiangxiensis—not yet formally described
A. kolomikta (Maxim. et Rupr.) Maxim.
A. kolomikta var. *gagnepaini* (Nakai) Li
A. laevissima C.F. Liang
A. laevissima var. *floscula* S.D.Shi
A. lanceolata Dunn
A. latifolia (Gardn. et Champ.) Merr.
A. latifolia var. *mollis* (Dunn) Hand.-Mazz.
A. leptophylla C.Y.Wu
A. liangguangensis C.F.Liang
A. lijiangensis C.F.Liang et Y.X.Lu
A. macrosperma C.F.Liang
A. macropserma var. *mumoides* C.F.Liang
A. maloides Li
A. maloides f. *cordata* C.F.Liang
A. melanandra Franch.
A. melanandra var. *cretacea* C.F.Liang
A. melanandra var. *kwangsiensis* (Li) C.F.Liang
A. melanandra var. *subconcolor* C.F.Liang
A. melliana Hand.-Mazz.
A. obovata Chun ex C.F.Liang
A. persicina R.H.Huang et S.M.Wang
A. petelotii Diels
A. pilosula (Finet et Gagnep.) Stapf ex Hand.-Mazz.
A. polygama (Sieb. et Zucc.) Maxim.
A. purpurea Rehder
A. rubricaulis Dunn
A. rubricaulis var. *coriacea* (Finet et Gagnep.) C.F.Liang
A. rubus H.Lév.
A. rufa (Sieb. et Zucc.) Planch. ex Miq.
A. rufotricha C.Y.Wu
A. rufotricha var. *glomerata* C.F.Liang
A. sabiifolia Dunn
A. setosa (Li) C.F.Liang et A.R.Ferguson
A. sorbifolia C.F.Liang
A. stellato-pilosa C.Y.Chang
A. strigosa Hook.f. et Thoms.
A. styracifolia C.F.Liang
A. suberifolia C.Y.Wu
A. tetramera Maxim.
A. tetramera var. *badongensis* C.F.Liang
A. trichogyna Franch.
A. truncatifolia C.Y.Chang et P.S.Liu
A. ulmifolia C.F.Liang
A. ulmifolia var. *flabellifolia* C.F.Liang
A. valvata Dunn
A. valvata var. *boehmeriaefolia* C.F.Liang
A. venosa Rehder
A. venosa f. *pubescens* Li
A. vitifolia C.Y.Wu
A. volubilis Sieb. et Zucc.
A. zhejiangensis C.F.Liang.

nearly 20% of all kiwifruit orchards are now planted in *A. chinensis*. The international kiwifruit industry of today, with more than 120,000 ha of orchard planted and with annual production exceeding 1.35 million t of fresh fruit, is based on these two *Actinidia* species. The word "kiwifruit" is thus no longer restricted to a single *Actinidia* species, *A. deliciosa*, or even, as was largely the case for many years, to a single cultivar, 'Hayward', of *A. deliciosa* (Ferguson 1999b). "Kiwifruit" is increasingly used for any species within the genus *Actinidia* and the term has become equivalent to the Chinese popular name for the genus, **猕猴桃**, or mihoutao. For example, "baby kiwifruit" or "hardy kiwifruit" are two of the names now used for *A. arguta* which, after a long lag period, now shows promise as the third *Actinidia* species to be established as a cultivated crop.

In this review, we therefore use kiwifruit to include any *Actinidia* taxon. The best known *Actinidia* species are *A. chinensis* and *A. deliciosa* but these are only two species of a genus which comprises some 76 species and about 125 taxa (Huang et al. 2000a,b) widely distributed throughout China and adjoining countries. Amongst these taxa, there is great diversity in infructescence size and in fruit characteristics such as size, shape, skin color, skin hairiness, skin toughness and palatability, flesh color, flesh texture, flesh flavor, flesh chemical composition, time of maturity (and hence time of harvest), and storage life, and changes in skin or flesh color and in flesh texture during ripening. There is likewise great diversity in other vine attributes: growth habit and vigor, climatic and soil requirements, time of budbreak, and of flowering, disease susceptibility, and yield potential; even ease of management. Furthermore, within a single taxon there can be considerable diversity. Species that are widely distributed are often polymorphic: morphological variants may be recognized although they may grade almost imperceptibly with one another through intermediate forms. Even if plants of the one taxon are indistinguishable morphologically they may still vary significantly in physiological responses if they come from very different habitats. Such variation could also be important in allowing the industry to respond to changes in climate or in allowing kiwifruit to be grown in new areas.

Such diversity provides the raw material for breeding and improvement programs. Obtaining information on this diversity is the first step towards the further exploitation of genetic resources for a sustainable world kiwifruit industry. Some of the information available has been reviewed previously (Ferguson 1990d). In the past decade, however, there has been intensive work on the interspecific and intraspecific variation within *Actinidia* of many horticulturally important traits, and on the natural distribution and habitats of taxa. Much of this new information has not previously been published or even summarized in English. Furthermore, recently developed techniques, especially molecular biology techniques, have helped us to understand better the relationships of the various *Actinidia* species. We believe, therefore, that it is timely to review what is known of the diversity within the genus.

We believe that it is also timely to record, before it is too late, details of the domestication of kiwifruit. An account of the development of the commercial kiwifruit industry based on *A. deliciosa* was published by Ferguson and Bollard (1990) but the industry has changed greatly since then. New Zealand no longer produces or even exports more kiwifruit than any other country; the supremacy of the cultivar 'Hayward' is being challenged; *Actinidia* species other than just *A. deliciosa* are now being cultivated; and the kiwifruit industry in China, original home of most *Actinidia* species, is developing rapidly. China now has more kiwifruit planted than any other country and could soon be playing an important part in the international trade in kiwifruit (Huang and Ferguson 2001, 2003). It is important to record such changes. Most crops have been domesticated for centuries or even millennia. Their origins and the natural distributions of their progenitor species are usually matters for conjecture and debate (see Frankel and Bennett 1970; Smartt and Simmonds 1995). In contrast, the domestication of *A. deliciosa*, the process by which it went from being a wild vine to an important horticultural crop, has occurred over the past one hundred years and almost every step in the process can be detailed. The domestication of *A. chinensis* is even more recent, with the process starting in China some 40 to 50 years ago. Now is the time to record that process before memories fade and information is lost.

II. GENETIC DIVERSITY AND GERMPLASM RESOURCES OF *ACTINIDIA*

A. Taxonomy, Geographic Distribution, and Evolution

1. The Genus and Infrageneric Subdivisions

> ". . . the conspicuous and exuberant variation in cultivated plants and their relatives has raised taxonomy problems that have never been solved nor adequately treated. The methods of classical taxonomy seem to fail altogether and inevitably result in establishment of dozens of epithets for races that are fully compatible when crossed." Harlan 1970

The genus *Actinidia*, Actinidiaceae, comprises 76 species and about 120 taxa in total. The systematic position of the genus has remained a matter of debate since the genus was erected, as have the subdivisions within the genus.

The early taxonomic history of the genus was summarized by Dunn (1911). The specimens of *Actinidia callosa* on which the genus is based were collected by Nathaniel Wallich, in Nepal, in 1821 and the new genus was described by Lindley (1836) who distinguished it by the climbing habit and by the radiating arrangement of the styles. Subsequently, specimens of congeneric species were collected by botanists or plant explorers in Japan, China, and Siberia, but were ascribed to different genera before it was recognised that they should all be placed in *Actinidia*. Gilg (1893) included 8 species in the genus, of which he listed 7, but made no mention of earlier described important species such as *A. chinensis*, *A. eriantha*, or *A. championi* (now *A. latifolia*). He split the 8 species into two groups according to the type of inflorescence (*Monanthae*—solitary vs. *Pleianthae*—cymes) but subsequent work showed that this classification could lead to the separation of males and females of an individual species. Extensive botanical collecting, mainly in inland China, meant that by 1895, 13 *Actinidia* species had been described and in 1911, Dunn, in the first systematic revision of the genus, considered 24 *Actinidia* species, some of which were further divided into varieties and forms. Dunn divided the genus into 4 sections, *Vestitae*, *Maculatae*, *Ampulliferae*, and *Leiocarpae*, based on the degree of pubescence, ovary shape, and the presence or absence of lenticels on the fruit surface (spotted or immaculate vs. non-spotted or maculate). In the next major revision, Li (1952) decided that the structure of the leaf hairs provided a clearer distinction, whereas degree of pubescence and ovary shape were relative characters that were not fundamental but showed considerable variation and were hence inadequate for defining major subdivisions within the genus. Li, therefore, divided the section *Vestitae* into two sections: *Stellatae* (those with stellate hairs) and *Strigosae* (those with simple hairs) and merged the *Ampulliferae* into the section *Leiocarpae*, but retained the section *Maculatae*. He listed 36 species, 9 of which contained varieties or forms.

The most recent revision by Liang (1984) considered only the taxa native to China but included many new taxa discovered during systematic investigations of *Actinidia* germplasm in each province. Liang retained Li's division into 4 sections but further subdivided the *Leiocarpae* into the series *Lamellatae* and *Solidae* on whether the pith of the stem was lamellate or solid, and the Stellatae into two series, *Perfectae* and *Imperfectae*, on the structure, frequency, and persistence of the stellate hairs. The current subdivision of the genus is therefore:

A	Leaves glabrous or only slightly hairy	
B	Fruit not spotted	Section *Leiocarpae* (Dunn) Li
C	Pith lamellate	Ser. *Lamellatae* C.F.Liang
CC	Pith non-lamellate	Ser. *Solidae* C.F.Liang
BB	Fruit spotted	Section *Maculatae* Dunn
AA	Leaves and branches very hairy	(Section *Vestitae* Dunn)
D	Coarse, hard simple hairs	Section *Strigosae* Li
DD	Fine soft hairs, stellate under leaves	Section *Stellatae* Li
E	Undersides of leaves have persistent stellate hairs	Ser. *Perfectae* C.F.Liang
EE	Undersides of leaves have imperfect or deciduous stellate hairs	Ser. *Imperfectae* C.F.Liang

There are, however, serious drawbacks to this subdivision of the genus. The separation of the *Imperfectae* from the *Perfectae* of the *Stellatae* indicates that possession of stellate hairs is not a particularly happy choice for subdividing the genus as the discovery of new taxa has shown that it also is a relative character. The degree of hairiness can be a subjective character. Solid pith is also found in some species outside the *Solidae*, so it is not a definitive characteristic. Furthermore, the *Strigosae* as defined by Liang is not a particularly satisfactory grouping because of the lack of morphological features common to the species within it, and the scattered distributions of the species (Liang 1983).

In his revision of *Actinidia*, Liang listed 51 species in China, 21 of which were further subdivided giving an additional 41 taxa: 35 varieties and 6 forms. Since that revision, *A. chinensis* has been split into 3 species (Liang and Ferguson 1986) with the previous infraspecific forms raised to varietal status and a further variety described. An additional 19 new species, 7 varieties, and 1 form have also been described (Gan 1983; Chang and Liu 1984; Liang 1982a,b, 1988, 1991; Liang and Lu 1989; Shi et al. 1994; Sun and Huang 1994; Huang and Wang 1995; Jiang 1995; Li et al. 2002b; Li et al. 2003a; Yu 1988). Conversely, *A. maloides* Li and

A. maloides f. *cordata* C.F.Liang have been reduced to *A. kolomikta* (Deng and Ming 2003). Several endemic taxa previously described from Taiwan are now thought to be not different to the mainland forms (Peng and Lu 1986 (2003); Lu 1996). When the species found only outside of China are included (*A. strigosa* from Nepal, *A. petelotii* from Vietnam, *A. hypoleuca*, and *A. rufa* from Japan and Korea, now also found in Taiwan), this gives a total of at least 75 *Actinidia* species in all, with 49 infraspecific taxa. Additional distinct variants have been recognised but not yet formally described (Cui et al. 2002).

More work, especially more comprehensive fieldwork, is required to determine whether all the species so far described are sufficiently distinct to justify separation at the specific level or whether, as is probable, it is more useful to revert to broader species concepts. Differences between species or between infraspecific taxa are not always large or consistent and there has been debate as to the level at which the differences observed justify separation of taxa, e.g., *A. arguta* and closely related taxa (Dunn 1911; Nakai 1933; Li 1952; Liang 1984). Furthermore, there may be consistent, if generally small, morphological differences between male and female plants of the same taxon, and there can also be considerable morphological variation in, for example, leaf size, shape and pubescence even within a single plant (Dunn 1911). Transitional forms suggest considerable hybridization between taxa with overlapping geographical distributions (Liang 1982b; Ferguson 1990a, 1990d), and some of the more recently described species may be natural hybrids, especially those whose descriptions are apparently based on a single genotype (Li et al. 2003a). It seems unwise to generalize conclusions from studies of only 1 or 2 individual genotypes of a particular taxon. Species that are widespread are often polymorphic and it may then be helpful to describe formally some of this variation as varieties or forms if they are clearly distinct and geographically separated. If the differences between variants are only small and if they grade one into another, then it may be better simply to accept that some species may be morphologically quite variable. This is in general the policy followed by Li et al. (2006) in their draft revision of Actinidiaceae for the new English version of *The Flora of China*.

Detailed morphological comparisons of the species indicate that the infrageneric subdivisions of the genus as modified by Liang (1984) are not sustainable. In particular, the *Maculatae* and the *Strigosae* seem to be heterogeneous and many of the characters delimiting these groups are found elsewhere in the genus (Condon 1991). Thus individual species within the *Maculatae* may have lamellate or solid pith, and the lenticellate fruit (possession of which is used to separate the *Maculatae* from the *Leiocarpae*) are also present in the sections *Strigosae* and *Stellatae*. Furthermore, there does not seem to be a clear distinction between simple and stellate hairs, but transitions between them (for example, in *A. cylindrica* var. *reticulata* and *A. sabiifolia*, both placed in the *Maculatae*) (Condon 1991; He et al. 2000a,b). Phylogenetic analysis based on the microscopic structure of the leaf hairs suggested that the *Leiocarpae* is a monophyletic group but that the *Maculatae* and *Stellatae* are polyphyletic (He et al. 2000a,b). Using cluster analysis of a much wider range of 50 morphological characters, Huang et al. (1999) proposed subdividing the genus into 3 sections: *Leiocarpae* retaining all species with smooth-skinned fruit, *Maculatae* including the species with spotted fruit and *Vestitae*, including all species with leaf hairs, which would be further divided into 2 series, *Stellatae* for species with stellate hairs on the undersides of the leaves and *Strigosae* for the species with simple and coarse leaf hairs. Li et al. (2000) suggested subdividing *Actinidia* into 2 subgenera, *Leiocarpae* and *Maculatae*, based on cladistic analysis of 22 morphological characters. Using solely morphological criteria, the *Leiocarpae* with their smooth-skinned, hairless fruit, seem consistently to form a reasonably coherent grouping. However, the subdivisions as proposed by Huang et al. (1999) and Li et al. (2000) left the *Maculatae* very heterogeneous, with individual species varying in type of leaf hair and frequency of lenticels on the fruit skin, making it difficult to delimit the sections.

Molecular studies have also confirmed that the subdivision of *Actinidia* as proposed by Liang cannot be sustained. Male and female plants of a particular taxon usually cluster closely in terms of genetic similarity (Li et al. 2003b) as do varieties within a species, although the lack of clustering of all varieties in species such as *A. callosa* and *A. fulvicoma*, both recognised as being morphologically polymorphic, indicates a need to reconsider some species boundaries (Huang et al. 2002a; Li et al. 2003b). Most studies show that the *Leiocarpae* are, in general, distinct from the remainder of the genus, but the subdivision of the other three sections seems artificial. Isozyme polymorphism in 8 enzyme systems (Testolin and Ferguson 1997) indicated that 3 species in the *Leiocarpae*, series *Solidae*: *A. macrosperma*, *A. polygama*, and *A. valvata*, formed a natural grouping as did 3 of the 4 species in the *Leiocarpae*, series *Lamellatae* studied: various forms of *A. arguta*, *A. hypoleuca*, and *A. melanandra*. *A. kolomikta* is usually placed in the *Lamellatae* because of morphological similarities, although it has yellow anthers whereas *A. arguta*, *A. melanandra*, and closely related species all have black anthers. On the basis of isozyme patterns, *A. kolomikta* seems only distantly related to the other species placed in the *Lamellatae*. Furthermore, in terms of leaf flavonoid composition, which has been very widely used in the chemotaxonomy of other plant genera, *A. kolomikta* is very different to the other species within the *Leiocarpae* studied (*A. arguta*, *A. hypoleuca*, *A. macrosperma*, *A. polygama*, and *A. valvata*) or, indeed, any other *Actinidia* species so far examined. RFLP analysis (Restriction Fragment Length Polymorphism analysis) of four regions of chloroplastic DNA likewise indicates that *A. kolomikta* is best treated as distinct from other members of the *Lamellatae* (Testolin et al. 1997; Cipriani et al. 1998). In contrast, however, RAPD analysis (Random Amplified Polymorphic DNA analysis) supports retaining *A. kolomikta* within the *Leiocarpae* (Huang et al. 2002a; Kim et al. 2003). It is clear that for elucidation of the relationships within the genus, evidence from a number of different approaches needs to be combined.

Although the accumulated evidence supports treating the *Leiocarpae* (apart possibly from *A. kolomikta*) as a monophyletic group, the section *Maculatae* appears to be a polyphyletic group with most members either as stand-alone single species or more closely related to individual members of the *Stellatae* or the *Strigosae* than to each other (Huang et al. 2002a). Conversely, individual species within the *Strigosae* or the *Stellatae* have a closer affinity to species in the other sections than to the others in their own section. The relationships between the different groups of *Actinidia* taxa are more easily understood if geographic distributions are considered.

2. Geographic Distribution. The genus *Actinidia* has a remarkably extensive distribution throughout much of eastern Asia, from just south of the Equator in the tropics, to cold temperate regions as far north as latitude 50° (Liang 1983; Cui 1993; Cui et al. 2002). Such a wide distribution is relatively uncommon among higher plants and means that *Actinidia* is a constituent of both the Holoarctic and Paleotropic floras.

The greatest abundance of taxa are in the provinces Yunnan, Guangxi, Hunan, Guizhou, Sichuan, Jiangxi, Zhejiang, Guangdong, Hubei, and Fujian followed by Shaanxi, Anhui, and Gansu (Liang 1983) (Fig. 1.1, Table 1.2). In this area are to be found not only the greatest number of taxa, but also the greatest diversity of infraspecific taxa (varieties or forms) and the greatest proportions of taxa endemic to a given province or region. These provinces are generally the richest floristically as well.

Liang (1983), therefore, defined the center of distribution of *Actinidia* geographically as being between the Yangzi (Chang Jiang) and Pearl (Zhu Jiang) Rivers, in a belt between approximately 25 to 30° north, including the Yunnan-Guizhou plateau toward the west, the hills and Nan Ling mountain range of south Hunan, and the hills along the

Fig. 1.1. Abundance of *Actinidia* taxa (species, varieties, and forms) within China. Taxa may be limited to only part of a province. Data derived from Table 2.

Table 1.2. Abundance of *Actinidia* taxa (species, varieties, and forms) by Chinese province and by country. Chinese provinces are listed from southwest to northeast in the order discussed in the text.

Country/Province	Total taxa	Endemic taxa
CHINA		
Yunnan	59	17
Guizhou	35	3
Sichuan & Chongqing	24	4
Xizang	6	0
Guangdong	25	2
Hainan	2	0
Guangxi	47	21
Hunan	38	1
Hubei	26	2
Henan	7	1
Anhui	12	0
Gansu	10	0
Shaanxi	14	1
Jiangsu	4	0
Zhejiang	21	2
Jiangxi	27	2
Fujian	19	1
Taiwan	8	1
Hebei	3	0
Shandong	3	0
Shanxi	3	0
Beijing	3	0
Liaoning	3	0
Jilin	3	0
Heilongjiang	3	0
NEIGHBORING COUNTRIES		
Russian Far East	3	0
Sakhalin and Kuril Islands	3	0
Japan	5	1
Korea	4	0
Cambodia	1	0
Laos	1	0
Vietnam	3	1
Myrnmar	2	0
Thailand	2	0
Malaysia/Indonesia	2	0
Northern India	2	1

Based on information in Chang and Liu (1984), Cui (1993), Cui et al. (2002), Deng and Ming (2003), Gan (1983), Hu et al. (2003), Huang and Wang (1995), Jiang (1995), Li (1952), Li et al. (2002b, 2003a), Liang (1975, 1982a,b, 1984, 1988, 1991), Liang and Lu (1989), Lin and Xiong (1991), Lu (1996), Shi et al. (1994), Yu (1988), and Zhao and Liu (1996). Several of the taxa listed in Cui et al. (2002) have not yet been formally described.

southeast coast. He concluded that this was probably also the center of current evolution of the genus.

This area of greatest abundance can also be defined climatically, a consequence of most *Actinidia* species growing best in warm, moist environments. The northernmost boundary of the area corresponds to the Qin Ling Mountains in southern Shaanxi, which are usually taken as the boundary between the dry, temperate north of China and the subtropical climate of the south. North of the Qin Ling Mountains, the climate is semi-arid and increasingly cold in winter (with mean temperatures in January below 0°C). Such conditions are unsuitable for most *Actinidia* taxa. Hence, there are no *Actinidia* at all to the northwest in Qinghai, Xinjiang, Ningxia, and Inner Mongolia. South of the Qin Ling Mountains the rainfall increases usually to at least 750 to 1000 mm and the humidity is higher. The western boundary corresponds to the lower mountains of the eastern border of the Tibetan plateau, the Hengduan Shan (Hengduan Mountains) to the west of Yunnan and Sichuan. Further west, as the land rises to the Tibetan plateau, rainfall and humidity drop, the mean annual temperatures fall dramatically, and frosts can occur almost any day of the year. Just as in the north, such cold, dry conditions are unsuitable for *Actinidia* species.

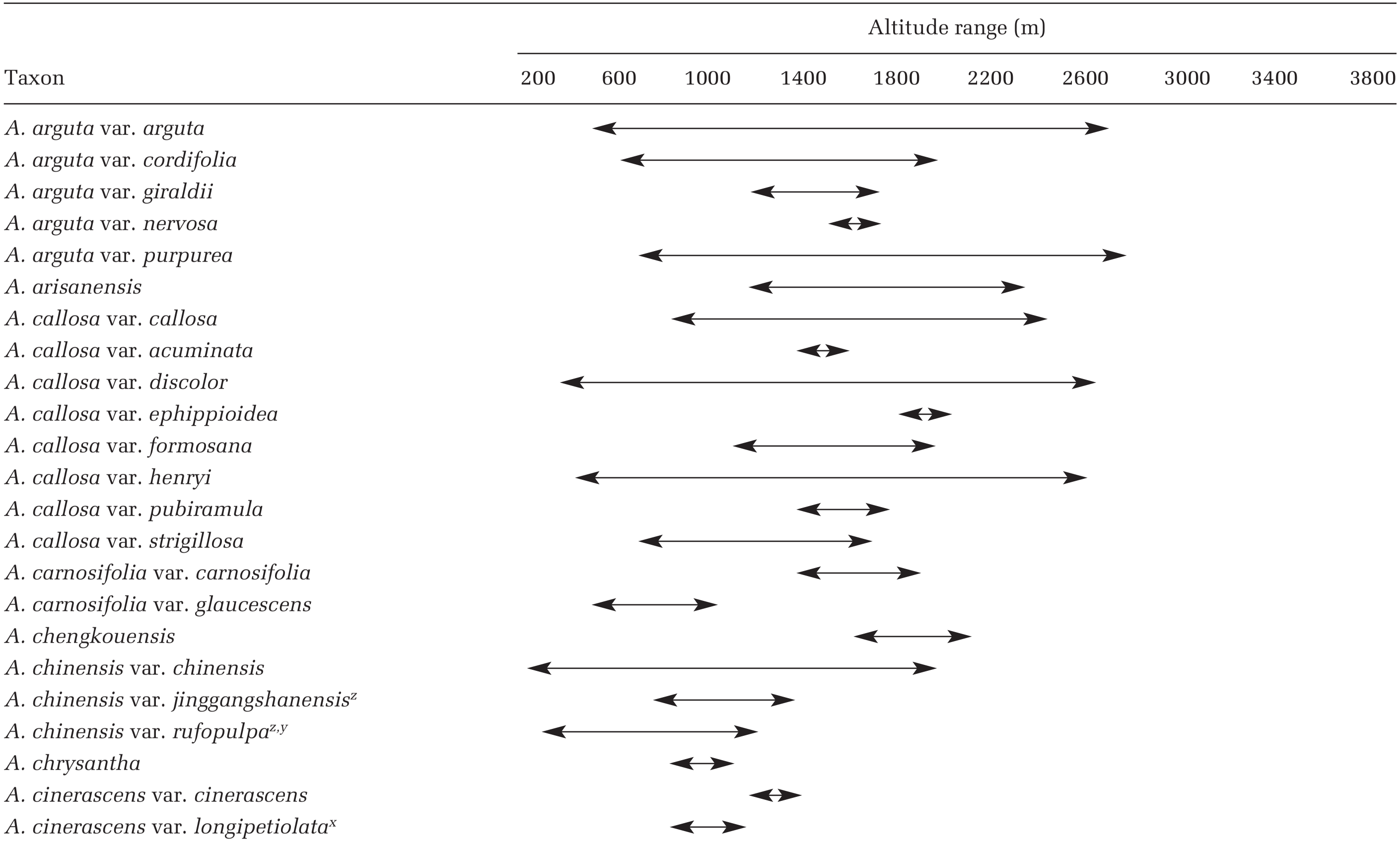
In south China, south of the isotherm that corresponds to a mean annual temperature between 20° and 22°C, temperatures seem too high for growth or fruiting and there are relatively few *Actinidia* taxa in the southern lowland regions of Guangxi, Guangdong, and Fujian. The mountains of Taiwan should provide suitable habitats, but, although the island is very close to mainland China, it has only 8 *Actinidia* taxa, one of which is endemic. Likewise, Hainan has only 2 *Actinidia* taxa, although its climate is more subtropical.

The general distribution pattern of *Actinidia* is typical of many components of the Chinese flora: great diversity within China itself and outlier taxa occurring in adjoining countries. Thus, *Actinidia* is also found westward to the Yarlung Zangbo Jiang (Yarlung Zangbo River) basin in Tibet and to the Himalayas in Northern India, eastward to the Japanese archipelago, north to Korea and Siberia, including Sakhalin, and, with several species south through Vietnam to Sumatra and Java near the Equator. Some of the taxa occurring in these countries are endemic or not found in mainland China itself, e.g., *A. hypoleuca*, *A. strigosa*, and *A. rufa*, but others are more cosmopolitan and found throughout much of the geographic range of the genus, e.g., *A. callosa* or *A. arguta*, although both of these have been divided into a number of distinct varieties, some of which are geographically separated. The exact taxonomic status of some of the *Actinidia* found in adjoining countries is uncertain.

3. Vertical Distribution. The altitudinal distribution of most *Actinidia* taxa in China was surveyed in detail during the nationwide survey of *Actinidia* germplasm (Cui 1980, 1993; Cui and Huang 1982; Cui et al. 2002). Taxa that occur over the greatest range of altitudes include *A. arguta* var. *arguta*, *A. arguta* var. *purpurea*, *A. callosa* var. *henryi*, *A. callosa* var. *discolor*, *A. kolomikta*, *A. melanandra*, *A. polygama*, *A. rubricaulis* var. *coriacea*, and *A. tetramera* (Table 1.3). The vertical distribution of a particular species is not absolute, but varies from location to location, based on the climatic requirements of the species as affected by latitude. A useful rule of thumb to predict the altitudinal range of a particular species at a given latitude, based on the accumulated experience of expeditions seeking and collecting wild germplasm, is that a change in latitude of 1° corresponds to a change in altitude of 100 m, or to a change of 0.6°C in monthly mean temperatures in spring and fall (L.-T. Zhang and H.-W. Huang, unpublished). Thus in different parts of their extensive geographic range, *A. arguta*, *A. kolomikta*, and *A. polygama* can be found from altitude 150 m above sea-level to 3500 m. Far to the north, in Heilongjiang province or in Siberia (50°N), these species may be found almost at sea level, but in southwestern China, in subtropical areas at the other extreme of their geographic range (25°N), they may be restricted to higher altitudes at 3000 m or even higher (for *A. kolomikta*, see Deng 2002). Similarly, at latitude 35°N, *A. deliciosa* is abundant at altitudes of about 1100 m, whereas further south, at latitude 25°N, it is found above 2300 m (Gao and Xie 1990). In contrast, taxa that occur over relatively limited areas in south China also have more restricted altitudinal distribution ranges: e.g., *A. cylindrica*, *A. glaucophylla*, *A. melanandra* var. *kwangsiensis*, *A. melliana*, and *A. zhejiangensis*, have very circumscribed distributions and generally are found only between 600 and 800 m.

4. Geographic Distribution and Reticulate Evolution. Geographic distribution of individual species appears to have played an important part in the evolution of the genus. If the subdivision of *Actinidia* by Liang (1984) is followed, the sections as he defined them differ markedly in their distributions (Dunn 1911; Liang 1983; Gao and Xie 1990). The *Leiocarpae*, the most morphologically consistent and distinctive grouping within the genus, is the only section to have many species north of the Huang He (Yellow River). These species are more cold-hardy and occur much farther to the north than do species from the other sections. The *Leiocarpae* also extend farther to the east and in southern, more subtropical regions, occur at higher altitudes, as in the Nan Ling Mountains in northern Guangdong and southern Jiangxi. This is well illustrated by Wu et al. (1987): in Hubei, the *Leiocarpae* are consistently at the higher

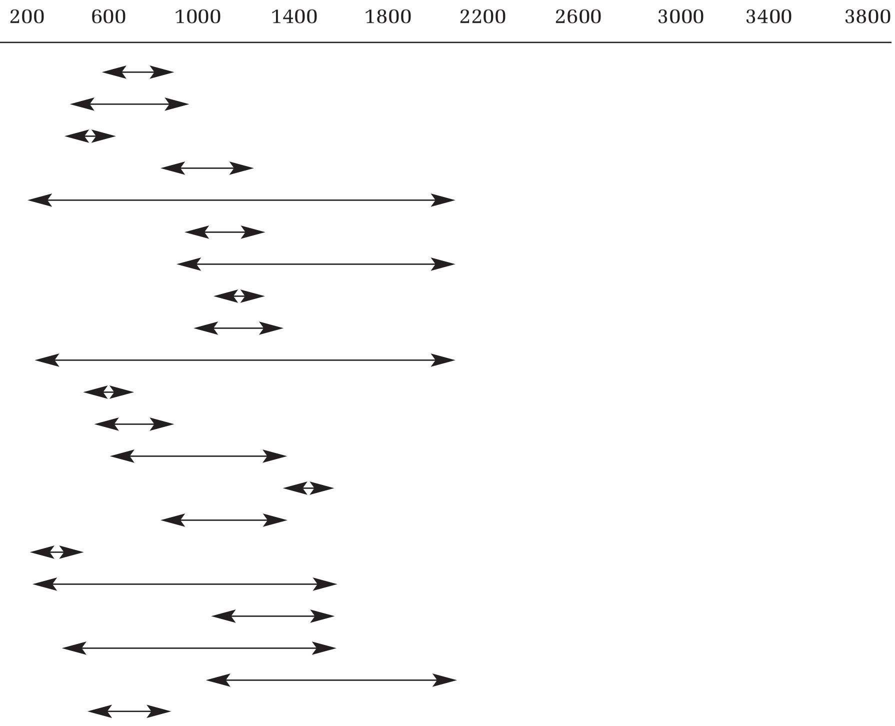
Table 1.3. Vertical distribution of *Actinidia* taxa in China.



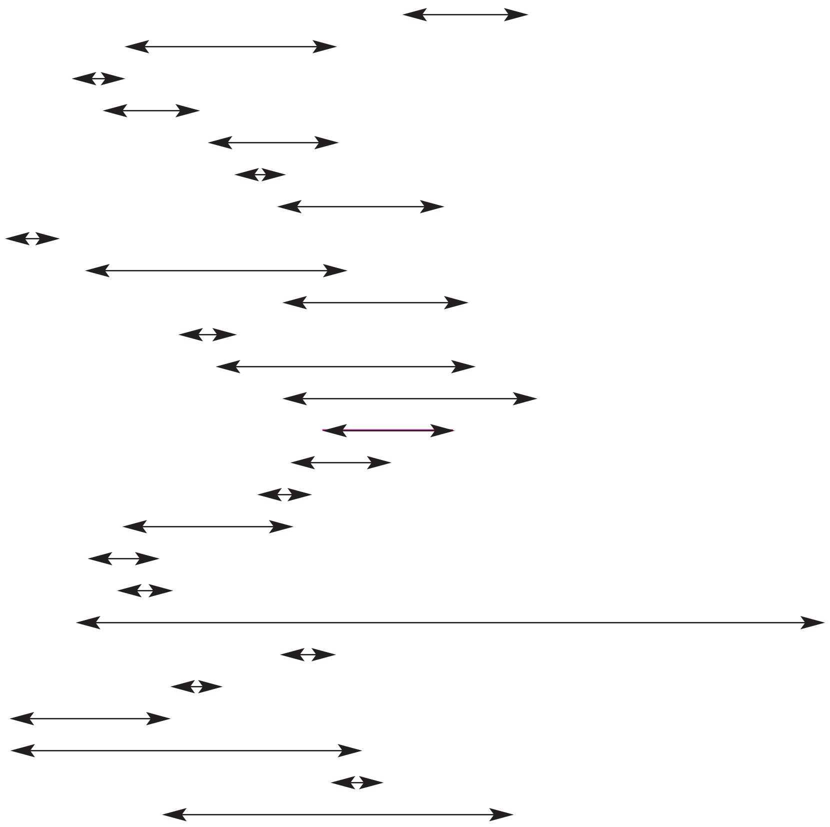
(*continued*)

Table 1.3. (*continued*)

Taxon	Altitude range (m)
A. cinerascens var. *tenuifolia*[r]	
A. cylindrica var. *cylindrica*	
A. cylindrica f. *obtusifolia*	
A. cylindrica var. *reticulata*	
A. deliciosa var. *deliciosa*	
A. deliciosa var. *changanensis**	
A. deliciosa var. *chlorocarpa*	
A. deliciosa var. *coloris*	
A. deliciosa var. *longipila*	
A. eriantha var. *eriantha*	
A. eriantha f. *alba*[w]	
A. fanjingshanensis[u,v]	
A. farinosa	
A. fasciculoides var. *fasciculoides*	
A. fasciculoides var. *cuneata*	
A. fasciculoides var. *orbiculata*	
A. fortunati	
A. fulvicoma var. *fulvicoma*	
A. fulvicoma var. *lanata*	
A. fulvicoma var. *lanata* f. *hirsuta*	
A. fulvicoma var. *pachyphylla*[x,t]	

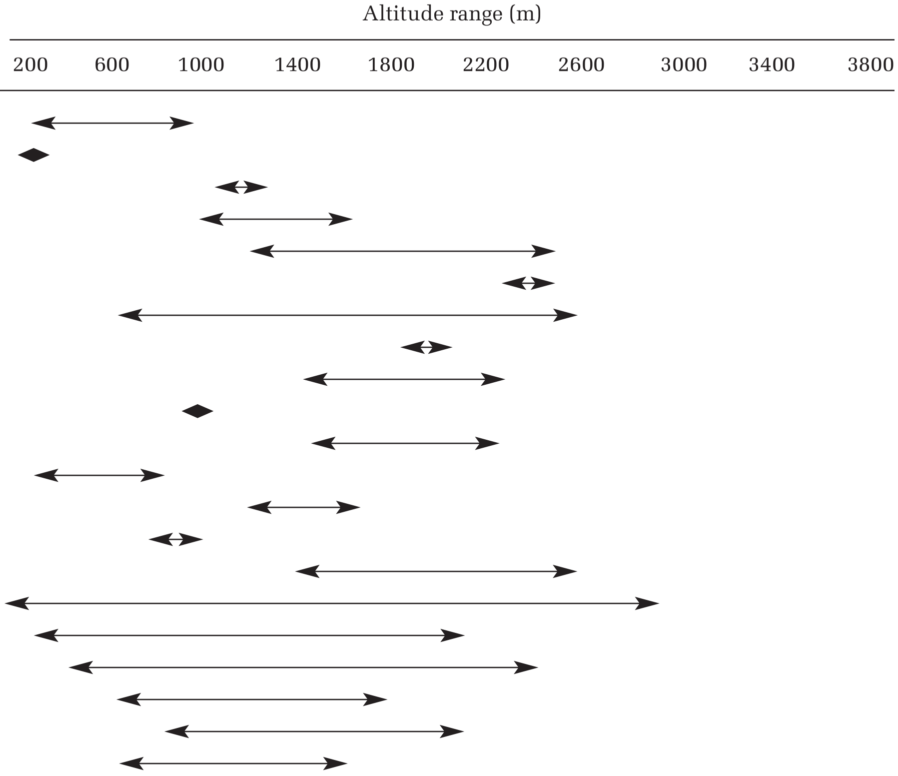


A. *glauco-callosa*
A. *glaucophylla* var. *glaucophylla*
A. *glaucophylla* var. *asymmetrica*
A. *glaucophylla* var. *robusta*
A. *globosa*
A. *gracilis*
A. *grandiflora*
A. *guilinensis*
A. *hemsleyana* var. *hemsleyana*
A. *hemsleyana* var. *kengiana*
A. *henanensis*
A. *henryi* var. *henryi*
A. *henryi* var. *glabricaulis*
A. *henryi* var. *polyodonta*
A. *holotricha*
A. *hubeiensis*[q]
A. *indochinensis*
A. *jiangkouensis*[v,u]
A. *jiangxiensis*[z]
A. *kolomikta*
A. *laevissima* var. *laevissima*
A. *laevissima* var. *floscula*[v,u]
A. *lanceolata* var. *lanceolata*
A. *latifolia* var. *latifolia*
A. *latifolia* var. *mollis*
A. *leptophylla*

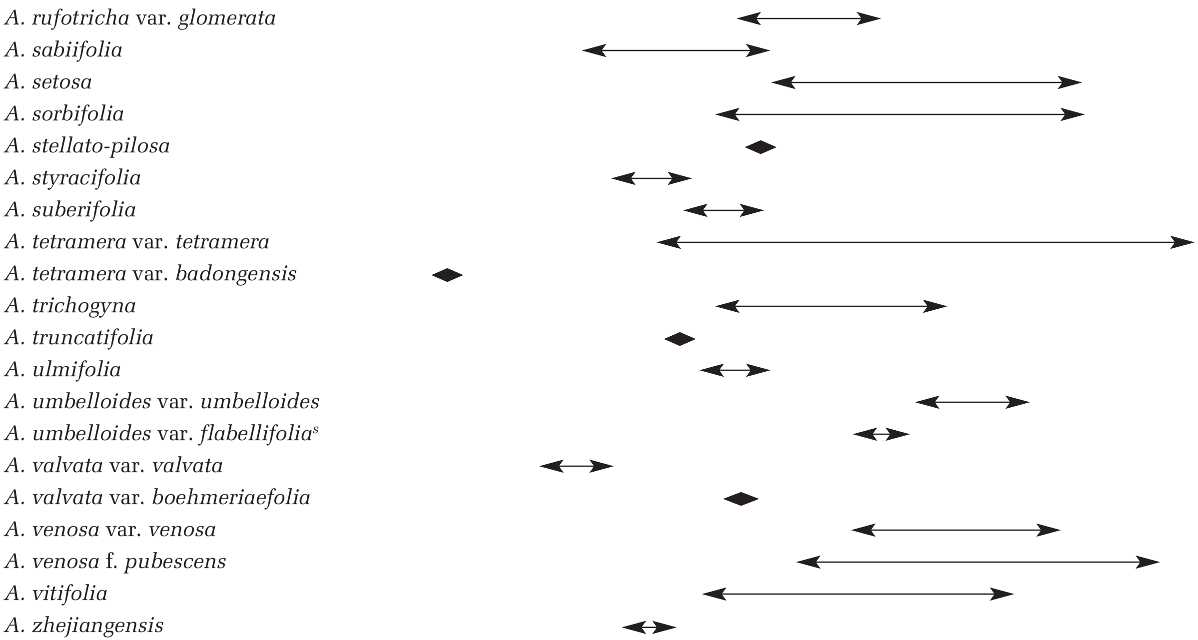


(*continued*)

Table 1.3. (*continued*)



Taxon
A. liangguangensis
A. lijiangensis
A. macrosperma var. *macrosperma*
A. macrosperma var. *mumoides*
A. maloides var. *maloides*
A. maloides f. *cordata*
A. melanandra var. *melanandra*
A. melanandra var. *cretacea*
A. melanandra var. *glabrescens*
A. melanandra var. *kwangsiensis*
A. melanandra var. *subconcolor*
A. melliana
A. obovata
A. persicina[p]
A. pilosula
A. polygama
A. rubricaulis var. *rubricaulis*
A. rubricaulis var. *coriacea*
A. rubus
A. rudis
A. rufotricha var. *rufotricha*



These data are taken from Cui (1993) with additional information from:

[z]Yao et al. (2005), [y]Liang (1982b), [x]Zhao and Liu (1996), [w]Qiu (1993), [v]Shi et al. (1994), [u]Dai et al. (2002), [t]Li (1952), [s]Liang (1984), possibly now extinct, [r]Xin et al. (1990), [q]Sun and Huang (1994), [p]Huang and Wang (1995).

*This taxon has not yet been formally described.

altitudes with species from other sections occurring lower down the mountains. Species in the *Leiocarpae*, therefore, have the distribution typical of the temperate flora of East Asia. Species that are widespread may be the oldest, whereas those that, morphologically, might be considered as more recently evolved or derived from natural hybridization (e.g., *A. globosa*, *A. henanensis*, or *A. macrosperma*) have relatively limited distributions.

The *Maculatae* are adapted to the colder, highland conditions in the west and their phylogenetic center is probably in the Yunnan-Guizhou plateau and the mountainous regions of western Guangxi. Some taxa extend west as far as the Himalayas and to the east in Taiwan and to Japan (if *A. rufa* is included in this section). Very few taxa in the section are found in the southeastern coastal regions of China. Appropriately, *A. callosa*, the species in the *Maculatae* with the most extensive distribution, overlapping those of almost all other species in the section, is also the species considered the most variable, having been divided into the greatest number of varieties. Most taxa in the *Maculatae*, especially those that might be considered as having evolved more recently, have more limited distributions to the southwest.

The *Strigosae* are generally better adapted to warm, humid conditions. Individual species are usually of very limited and scattered distributions, overlapping those of species in the *Maculatae*.

The *Stellatae* constitute the most southern part of the genus. The two best-known species, *A. chinensis* and *A. deliciosa*, extend well to the north with the northern limit for *A. deliciosa* being the Qin Ling Mountains (Shaanxi Province). However, most species in the *Stellatae* occur south of the Yangzi River, indicating their association with the subtropical flora of Southeast Asia. The center of speciation of the *Stellatae* appears to be Guangdong, Guangxi, and the southeastern part of the Yunnan-Guizhou plateau. One species, *A. latifolia*, extends southward as far as the Equator.

However, this analysis (Liang 1983) is probably too simplistic: as discussed above, Liang's *Maculatae*, *Strigosae*, and *Stellatae* all appear to be polyphyletic. Most studies using cluster analysis dendrograms and strict consensus trees based on morphological characters and DNA markers (Huang et al. 1999; Li et al. 2000; He et al. 2000a; Li et al. 2002a; Huang et al. 2002a; Li et al. 2003b) associated many of the *Actinidia* species into geographic groupings corresponding to north China, the Yangzi River Valley, southeastern China, southern China, and southwestern China. For example, *A. eriantha*, *A. fulvicoma*, and *A. styracifolia* formed a cluster centered in Fujian and Guangdong, extending to Guangxi and Guizhou; *A. farinosa*, *A. rufotricha*, *A. glaucophylla*, *A. liangguangensis*, *A. cylin-*

drica, *A. chrysantha*, and probably *A. indochinensis*, formed another cluster centered in Guangxi and Guizhou and spreading into Guangdong and Hunan; and *A. chinensis*, *A. deliciosa*, *A. lijiangensis*, *A. hubeiensis*, *A. grandiflora*, and *A. callosa* var. *strigillosa* made up another grouping mainly centered on the Yangzi Valley (Huang et al. 2002a).

Allopatric or geographic speciation, in which new species arise when populations are reproductively separated by geographic barriers, has often been suggested as one of the most important mechanisms responsible for the evolution of new plant species (Mayr 1942). Other isolation mechanisms (Nei 1987) include ecological separation, differences in time of flowering, self-compatibility and ploidy variation. Although no one individual isolation mechanism is necessarily more effective than any other (Harlan 1970), it is very probable that several isolation mechanisms acting in combination could result in much more complex patterns of evolution than would a single mechanism acting alone. The very broken topography of southwestern and central China, the diverse soil conditions, and the very variable microclimates, as influenced by the mountain ranges of these regions, have probably encouraged increased rates of speciation. Studies on the *Actinidia* taxa in Hunan show that the greater the environmental diversity, the greater the number of taxa present (Zhao and Liu 1996). On the basis of topography and the number and diversity of taxa, southwestern and central China, which contains about 60% of all *Actinidia* species, is probably the current center of evolution of the genus (Liang 1983). Thus, the patterns of geographic distribution associated with speciation justify serious consideration in any revision of the genus.

Polyploidy has long been recognized as a major driver of evolution in plants, but in recent years there has been an increasing realization that recurrent polyploidization is the rule, not the exception, and that lineages of recurrent origin can vary morphologically (Soltis and Soltis 1999; Soltis et al. 2003). In *Actinidia*, there is a reticulate pattern of diploids, tetraploids, hexaploids, and octoploids (see Section II.D.1) and it is likely that this, combined with recurrent polyploidization and frequent hybridization among geographically overlapping species, has resulted in a reticulate evolutionary structure in the genus (Huang et al. 2002a). In nature, there is probably considerable gene flow between species despite differences in ploidy since artificial hybridization is frequently successful (Wang et al. 1989, 1994; Ke et al. 1992; An et al. 1995; Cipriani et al. 1995; Ferguson et al. 1996; Chat et al. 1999; Hirsch et al. 2001). Although other explanations are possible, one indication of reticulate evolution is incongruence between different independent markers coming from the nucleus and an organelle such as the chloroplast. Thus, *A. eriantha* and *A. latifolia* are morphologically distinct (Li 1952; Liang 1984) and are also distinct in terms of flavonoid composition (Webby et al. 1994) and isozyme analysis (Testolin and Ferguson 1997), all characters dependent on nuclear genes; but the two species seem very closely related in terms of chloroplastic DNA sequences (Testolin et al. 1997; Cipriani et al. 1998). Likewise, *A. chinensis* and *A. indochinensis* are clearly distinct morphologically and according to isozyme analysis, but show few differences in chloroplastic DNA (Testolin et al. 1997). It was concluded that in such cases, one species of each pair is a hybrid having the second species, or one with a similar plastome, as the male parent. In *Actinidia*, chloroplasts are usually inherited from the father and mitochondria from the mother (Cipriani et al. 1995; Testolin and Cipriani 1997; Chat et al. 1999), although in some controlled interspecific crosses it seems that chloroplasts may be inherited from the mother (Jung et al. 2003b). Such complementary paternal and maternal inheritance patterns provide an exceptional opportunity for studying phylogeny in *Actinidia* (Cipriani et al. 1998). Although only limited information is so far available from mitochondrial DNA sequences, Chat et al. (2004) were able to conclude that at least 12 of the 41 *Actinidia* taxa they studied (diploids, tetraploids, and 1 hexaploid) had undergone hybridization at least once in their evolutionary history. Furthermore, 8 of the species studied were represented by two or more infraspecific varieties: 5 of these species, *A. callosa*, *A. cylindrica*, *A. deliciosa*, *A. eriantha*, and *A. glaucophylla* proved to be polyphyletic in their chloroplastic DNA, in their mitochondrial DNA or, in two cases, in both chloroplastic and mitochondrial DNA (Chat et al. 2004). Such results indicate that *Actinidia* is similar to many other plants in that "polyploid genomes and genome evolution may be far more complex than . . . imagined previously" (Soltis et al. 2003). One difficulty is that so far only a very small number of genotypes have been studied for each taxon, and these genotypes were not necessarily typical or included all the phylogenetic variation within the taxon.

The abundance of rather ill-defined *Actinidia* taxa often lacking discrete taxonomic boundaries and the intermingling of characters, both morphological and molecular, is thus probably due to the frequent occurrence of hybridization, more frequent than often assumed (Chat et al. 2004), and reticulate evolution as influenced by geographic patterns of distribution. Liang's *Leiocarpae* is most probably an ancestral group: the species *A. polygama*, *A. valvata*, and *A. kolomikta* could be considered progenitor species, and *A. arguta*, *A. melanandra*, and *A. macrosperma* considered more recent derivative species which are still undergoing rapid speciation since they are more variable species and contain more infraspecific taxa (Liang 1983). The species with spotted fruit (Liang's *Maculatae*) could be considered as a parallel lineage group to the *Leiocarpae* and could represent a transition from the progenitor species with smooth-skinned fruit (*Leiocarpae*) to pubescent species (most species in Liang's section *Stellatae* have hairs on the fruit skin to at least some extent). Imposed on this transition are the effects of geographic, spatial, and vertical distribution, heterogeneous environments, mutation, and natural, possibly recurrent, hybridization resulting in geographically oriented, polyphyletic groups of species including those in Liang's sections *Stellatae* and *Strigosae*. For this reason, the infrageneric subdivisions of *Actinidia* should take into account the geographic distributions of the species, particularly those currently placed in Liang's *Maculatae* and *Stellatae*. The best and most natural solution may be to divide *Actinidia* into two sections *Leiocarpae* and *Maculatae*, the latter then being further divided into 4 series containing taxa from the Yangzi Valley, southeastern, southern, and southwestern China.

5. The *A. chinensis/A. deliciosa* Complex. There is no disagreement that *A. chinensis* and *A. deliciosa* are closely related: rather, any discussion is as to whether the differences between them are sufficient to justify their being considered separate species (e.g., Xiong 1991; Hirsch et al. 2002; Huang et al. 2002a; Li et al. 2003b, Chat et al. 2004) and as to whether *A. deliciosa* is allopolyploid or autopolyploid in origin.

When these two species were initially separated (Liang and Ferguson 1984) following up the suggestion by Gui (1981), Liang Choufen, who had an unequalled knowledge of the morphological diversity within *Actinidia* in China, considered that the differences were comparable to those he had used to discriminate between other species, although initially he had treated *A. chinensis* and *A. deliciosa* as varieties of the one species (Liang 1975, 1982b). Furthermore, there seemed a clear distinction in ploidy with *A. chinensis* being diploid and *A. deliciosa* hexaploid. Since then, the distinction between the species has become somewhat less clear-cut with the discovery of tetraploid as well as diploid races in *A. chinensis* (Xiong 1992; Yan et al. 1994) (*see* Section II.D.2), the identification of some intermediate or hybrid forms (Liang 1982a,b), and the recognition of a number of other closely related species. Furthermore, the differences between *A. chinensis* and *A. deliciosa* revealed by RAPD analyses (Huang et al. 2002a) seem more consistent with separation at the infraspecific level than at the specific level (see also Jia et al. 2005; Li et al. 2006).

A. chinensis and *A. deliciosa* cannot be distinguished by their flavonoid composition, whereas most other *Actinidia* species studied contain unique combinations of flavonoids (Webby et al. 1994). Likewise Hirsch et al. (2002) found two coumarins, esculin and fraxin, only in *A. chinensis* and *A. deliciosa* but not in 8 other *Actinidia* species (mainly from the *Leiocarpae*). These studies support the conclusion based on morphological studies that the 2 species are indeed closely related.

There is agreement that diploid *A. chinensis* is almost certainly a progenitor of *A. deliciosa* but there is still no clear consensus as to whether any other *Actinidia* species have also contributed genomes. Isozyme analysis (Testolin and Ferguson 1997) of 40 alleles in *A. chinensis* and in *A. deliciosa* showed that of the alleles studied, 34 (85%) were in both species and the alleles that were in only 1 or other of the 2 species were those for highly polymorphic enzyme systems. It was therefore suggested that *A. deliciosa* was an autopolyploid which could have arisen from the polyploidization of *A. chinensis*, especially as there was no species that could supply all the alleles found in *A. deliciosa* without also contributing other alleles indicative of that species. Restriction site variation in PCR (Polymerase Chain Reaction)-amplified chloroplast DNA regions likewise indicated that *A. chinensis* and *A. deliciosa* were very closely related and, since in *Actinidia* chloroplasts are usually inherited solely from the male parent, that *A. chinensis* was the paternal, if not the only progenitor of *A. deliciosa* (Cipriani et al. 1998). Similarly, sequencing of nuclear ribosomal DNA internal transcribed spacers and the chloroplast *matK* gene gave no indication that *A. deliciosa* was allohexaploid (Li et al. 2002a). Studies using microsatellite (Simple Sequence Repeat) markers likewise indicated that *A. chinensis* is the sole progenitor of *A. deliciosa* (Zhen et al. 2004).

Other evidence, however, is most easily explained by assuming that *A. deliciosa* is indeed allopolyploid. It forms bivalents at meiosis, although this could be due to "diploidization" after allopolyploid formation, or to the existence of a meiotic pairing control system (McNeilage and Considine 1989). More convincing, allelic segregation at 10 isozyme loci in the progeny of a cross *A. deliciosa* (6*x*) × *A. chinensis* (2*x*) and in progeny of a cross *A. chinensis* (4*x*) × *A. eriantha* (2*x*) indicated that *A. deliciosa* was an allohexaploid, but that the tetraploid forms of *A. chinensis* studied were autoploid (Huang et al. 1997). RFLP analysis confirmed the close relationship between *A. chinensis* and *A. deliciosa* (Crowhurst et al. 1990) but indicated that another species must be involved in the origin of *A. deliciosa* as it contained a family of repeat sequences not present in diploid *A. chinensis* (Crowhurst and Gardner 1991). Phylogenetic analysis of DNA sequences from the polygalacturonase gene likewise indicated that *A. deliciosa* was allopolyploid but also indicated that the particular tetraploid *A. chinensis* studied was similarly allopolyploid (Atkinson et al. 1997). Dot blotting and genomic in situ hybridization using the specific repeat sequence probe pKIWI1516 used by Crowhurst and Gardner (1991) showed that the repeat sequence could not be detected in most species checked, including diploid *A. chinensis*, but was present in *A. chrysantha* and *A. deliciosa* and in some, but not all, tetraploid *A. chinensis* studied, with six discrete hybridization sites identified (Yan et al. 1997a). There appeared to be at least two distinct genomes in some but not all tetraploid *A. chinensis* and in *A. deliciosa*, one genome with and the other without the repeat sequence. The evolutionary histories of these two groups of tetraploid *A. chinensis* are clearly different (Murray 2002). There is no other evidence suggesting that *A. chrysantha* is closely related to *A. chinensis* and *A. deliciosa* and it is therefore unlikely that it has contributed to the genome of *A. deliciosa*. Further work using a greater range of diploid and tetraploid genotypes of *A. chinensis* and *A. deliciosa* from different parts of the geographic range in China could be rewarding.

A number of species of mainly limited distributions are considered to be morphologically close to *A. chinensis* or *A. deliciosa*, for example, *A. chengkouensis*, *A. hubeiensis*, *A. obovata*, *A. setosa*, *A. sorbifolia*, and *A. stellatopilosa*. It has been suggested that some are possibly natural hybrids, for example *A. chengkouensis* might be a hybrid between *A. deliciosa* and a species from the *Strigosae*; and *A. stellatopilosa* might be a hybrid between *A. deliciosa* and *A. trichogyna* (Liang 1984). Likewise, *A. hubeiensis* might be a hybrid between *A. chinensis* and a member of the *Maculate* such as *A. callosa* (Sun and Huang 1994). *A. setosa* was originally included as a variety of *A. chinensis* s.l. (Li 1952) but chloroplastic and mitochondrial DNA sequence studies suggest that it has diverged from *A. chinensis* and *A. deliciosa* (Chat et al. 2004). More detailed studies, including molecular studies, of a much greater range of genotypes of these species could prove helpful. Any revision of the status of *A. chinensis* and *A. deliciosa* must take account of these related species if the revision is to be useful.

6. The Problem of *A. rufa*. The Japanese plant, shima-sarunashi, now associated with the name *A. rufa* has been variously placed in this species, in *A. arguta* and in *A. callosa*. Without examining the herbarium specimens used, it is difficult to understand why both Dunn (1911) and Li (1952) considered that *A. arguta* var. *arguta* and what is now generally accepted as *A. rufa* (Ohwi 1965, Walker 1976) were varieties of the one species, irrespective of which name should actually be applied to the whole species. Living plants of *A. arguta* and *A. rufa* are very different in their vegetative morphology, in their flowers, and their fruit. In particular, the shoots, young leaves, sepals, and the fruit of *A. rufa* are covered by a fine, but dense, reddish-brown tomentum, whereas those of *A. arguta* are essentially glabrous. Furthermore, *A. arguta* has purple-black anthers, whereas those of *A. rufa* are yellow. At least some of the herbarium specimens used must have been misidentified as Li (1952) describes the anthers of what he called *A. arguta* var. *rufa* as being purple-black not yellow. Liang (1984) did not consider *A. rufa* in his treatment of the *Actinidia* species from China but accepted it as being a quite distinct species (C.-F. Liang, person. commun.). It has since been identified as being present in Taiwan (Peng and Lu 1996). The exclusion of *A. rufa* from the *Leiocarpae* on morphological characteristics (Condon 1991) is supported by studies on leaf hairs (He et al. 2000a,b), flavonoid composition (Webby et al. 1994), isozyme patterns (Testolin and Ferguson 1997), chloroplast and ribosomal DNA sequences (Cipriani et al. 1998; Li et al. 2002a; Chat et al. 2004) and RAPD analyses (Huang et al. 2002a; Kokudo et al. 2003; Li et al. 2003b). The species is probably best placed in the *Maculatae* but RAPD analysis (Li et al. 2003b) and sequence data (Chat et al. 2004) indicate that it could be closely related to the entity named *A. persicina* by Huang and Wang (1995) (*Stellatae*, *Perfectae*), and to *A. zhejiangensis* (*Stellatae*, *Imperfectae*), and *A. hemsleyana* (Strigosae). However, Jung et al. (2003a) disagreed, placing *A. rufa* close to *A. kolomikta* and *A. melanandra* because of similarities in noncoding chloroplastic DNA sequences. Morphologically, however, there are a number of similarities between *A. rufa* and *A. callosa* var. *henryi*.

B. Variation in Fruit Characteristics

There is tremendous genetic variation at both the interspecific and infraspecific level within *Actinidia* in vegetative, floral, and fruit characteristics (e.g., Li 1952; Li et al. 1996). Since fruit traits are the main concern to horticulturists and plant breeders for germplasm management and cultivar improvement, we concentrate on some aspects of fruit variation (Li 1952; Huang et al. 1983; Liang 1984; Li et al. 1985; Ferguson 1990d; Huang et al. 2000a,b, 2004; Cui et al. 2002; Han et al. 2003).

1. Fruit Size. Fruit size is one of the most important initial criteria in determining which *Actinidia* species have commercial potential. Most species have fruit that are much smaller than those of wild-growing vines of *A. chinensis* and *A. deliciosa* or of commercialized kiwifruit cultivars (Plate 1.1B).

The smallest fruit in the genus are those of *A. maloides* Li weighing each about 0.5–0.7 g; the largest are those of *A. chinensis* and *A. deliciosa* (Huang et al. 2004). The estimates of fruit size given are often from wild plants, in which nutrition or pollination may be sub-optimal, or from individual, not necessarily typical, plants in germplasm collections. Considerably bigger fruit might be achieved on cultivation, but fruit size in individual selections will depend on growing conditions, pollination, and intensity of thinning or may be affected by application of plant bioregulants. The maximum fruit weights quoted are sometimes those for fasciated fruit. Within an individual species there can be great variation in fruit size, e.g., Cheng et al. (2005) found a range in mean fruit size from 14.4–127.6 g in a population of 289 female *A. chinensis* vines arising from a factorial crossing of 3 females by 13 males, although these were parents from different seed accessions. Similar ranges might be expected in natural populations.

Fruit of *A. chinensis* from the wild tend to be slightly smaller on average than those of *A. deliciosa*, sometimes less than 15 g mean fruit size, but individual selections can have fruit at least the size of *A. deliciosa* 'Hayward', up to 7 cm long by 5.5 cm in diameter; up to 110 g mean weight with some fruit much larger. Fruit of the *A. chinensis* selection 79-1-1 averaged 160 g when it was grown in New Zealand, although this average weight could decrease as the vines mature and carry heavier fruit loads. The maximum fruit size in *A. chinensis* is probably the same as in *A. deliciosa*, with a mean fruit weight of 180–200 g possibly achievable.

'Hayward' and 'Qinmei', the two most widely grown cultivars of *A. deliciosa*, have large fruit consistently averaging about 110 g, but some selections have even larger fruit, e.g., 'Jade Moon' (a natural mutation of 'Hayward') with a mean fruit size of c. 115–120 g. The other species with the largest fruit, such as *A. chengkouensis*, *A. eriantha*, *A. grandiflora*, and *A. setosa*, are generally those closely related to *A. chinensis* and *A. deliciosa*.

Fruit size also depends on position within the infructescence. The largest infructescences are those of *A. guilinensis* and *A. latifolia* which can include 30 fruit. In other species, fruit occur either singly or more commonly in an infructescence of 3 or 5, with the terminal or "king" fruit being larger than the lateral fruit. Selection for fruit size is usually accompanied by selection for fruit occurring singly, thereby decreasing the within-vine variability in fruit size. This has the associated advantage of reducing the damage due to windrub on contiguous fruit. The number of flowers (and hence the number of fruit) at each axil can vary with climatic conditions (Ferguson 1990d). The behavior of a particular genotype can therefore be drastically modified by comparatively small differences in climatic conditions. Within infructescences, individual fruit tend to ripen and soften at different rates.

2. Fruit Shape. *Actinidia* fruit are generally ovoidal or spheroidal (Li 1952; Liang 1984; Li et al. 1985; Ferguson 1990d; Huang et al. 2000b, 2004; Cui et al. 2002). However, at least 15 different fruit shape descriptors have been used to describe the variation within the genus: ovoid-globose, obloid, globose, oblong, near globose, ellipsoid, short cylindrical, cylindrical, ovoid, obovoid, long globose, ovoid-cylindrical, long cylindrical, long conoidal, ovoid-conoidal, and ovoid-globose (Huang et al. 2004). The UPOV (2001) descriptors for kiwifruit indicate that, in addition, the fruit shape in cross section, the taper to the stalk or stylar end, the squareness of the shoulders, and the general shape of the stylar end can be used to distinguish cultivars. A strong protrusion of the stylar end or "beak" is characteristic of *A. polygama* fruit and of individual cultivars such as *A. chinensis* 'Hort16A' and *A. deliciosa* 'Qinmei' (for photographs, see Ferguson 1999a; Cui et al. 2002).

3. Fruit Hairs and Skin. Fruit in the *Leiocarpae* (e.g., *A. arguta*, *A. melanandra*, and *A. polygama*) have smooth skins and appear essentially glabrous with only infrequent, simple hairs (Liang 1984; Huang et al. 2004; Hallett and Sutherland 2005). Other species in the genus have fruit with varying degrees of pubescence ranging from apparently glabrous up to the long, very stiff hairs of *A. setosa* (Huang et al. 2004) (Plate 1.1B, 1.1C, 1.1D, 1.2A).

The best-described hairs are those of *A. deliciosa* which occur as two types intermixed: multiseriate, tapering hairs with very long apical cells and much shorter, uniseriate hairs that may be arrested stages in the development of the longer hairs (White 1986a). Different cultivars of *A. deliciosa* show considerable variation in fruit hairs, ranging from downy (e.g., the selection 'Downy') to bristly or setose (e.g., 'Bruno') to hispid (e.g., 'Hayward') reflecting differences in the relative abundance of the two types of hairs and the dimensions of the larger hairs (White 1986b). Mutations can result in hair loss. Top Star® is a bud mutation of *A. deliciosa* 'Hayward' in which the fruit are essentially hairless, but the fruit look "naked" and the skin is not particularly attractive and is generally regarded as being unpalatable. Many genotypes of *A. chinensis* have fine hairs, almost like the bloom on a peach, and in the case of 'Hort16A' this is due to there being fewer of the multiseriate larger hairs (which in this cultivar are also smaller), and a greater density of the small, uniseriate hairs (Hallet and Sutherland 2005). Of the *Actinidia* species that have hairs on their fruit, at one extreme there are the fruit of *A. rufa*, which are puberulent or minutely pubescent, and at the other extreme, the fruit of *A. eriantha* or *A. zhejiangensis*, which are tomentose to lanate. Electron microscopy shows that the fruit surface of *A. rufa* has only small, uniseriate hairs, very similar to the smaller hairs on the fruit of *A. deliciosa* or *A. chinensis*. Fruit of *A. eriantha* have both small, uniseriate, two-celled hairs with a long tapering apical cell and abundant, much longer, slender, multicelled hairs, often branching near the base to form a cluster of 3 hairs, each terminating in a very long thin apical cell (White 1986b).

The long coarse hairs of cultivars such as *A. deliciosa* 'Hayward' are generally considered a fault, a disadvantage to consumers that should be selected against. Such hairs can, however, protect the developing fruit from mechanical damage or some insect pests and are largely removed by brushing and during grading in packhouses. The fine soft hairs on the fruit of many *A. chinensis* selections can make the fruit initially appear more attractive; the hairs are not really a disadvantage as most consumers find the fruit skin unpalatable. However, such fine hairs are often easily lost in patches when rubbed and this is a drawback because the fruit then appear superficially damaged and less attractive. In some species, the hairs are not persistent at maturity, and this can be a definite disadvantage, e.g., as in ripe fruit of some *A. eriantha* genotypes that can look as if their long, white fur is molting.

Actinidia fruit hairs, if present, are generally yellowish-brown to gingerish to reddish-brown (White 1986b; Cui et al. 2002) with the most notable exception being the pure white hairs of some *A. eriantha* selections. The underlying fruit skin can be dark green or light green to brown to reddish-brown with the light brown to reddish-brown skins often more attractive than those with an underlying greenish tinge or those that are dark brown. The fruit skins may appear spotted because of the prominent lenticels (for photographs see Cui et al. 2002). Fruit skins of species in the *Leiocarpae* have almost no hairs and are a smooth, unspotted, shiny green. As such fruit ripen they may develop a reddish blush (e.g., some selections of *A. arguta*, Hassall et al. 1998), or become yellow (*A. polygama* and *A. tetramera*), orange (*A. macrosperma* and *A. valvata*), reddish (some *A. melanandra* and *A. henanensis*) or purple (*A. arguta* var. *purpurea*) (Huang et al. 2004). Such color changes may be superficial but are more often due to changes in the underlying pericarp.

The fruit skins of species in the *Leiocarpae* are edible if somewhat chewy and, depending on the species or the genotype, rather similar to the skins found on some grapes. Even so, *A. arguta* has been crossed with *A. deliciosa* in an attempt to breed large kiwifruit with smooth, hairless skins (White and Beatson 1993). Soft skins, as in *A. arguta*, however, make fruit more susceptible to mechanical damage and more prone to water loss, and hence shriveling, on ripening and storage (Hassall et al. 1998).

Detailed information on the structure of *Actinidia* fruit skins explains why only some skins are palatable (Hallett and Sutherland 2005). Fruit of *A. arguta* have a simple skin consisting of an epidermis with thick cuticle and underlying hypodermis (and no hairs) and are hence edible, whereas those of *A. chinensis* 'Hort16A' and *A. deliciosa* 'Hayward' are usually considered unpalatable because of the hairs and a thick layer of dead, radially compressed cells with suberized walls external to the hypodermis. In 'Hort16A', but not 'Hayward', there is also a fragile layer of thin-walled cells and stone cells between the hypodermis and the outer pericarp. A fundamental difference between *A. chinensis* and *A. deliciosa* is unexpected and this may be a distinction between individual genotypes rather than between species. The skin of *A. eriantha* is more easily removed from ripe fruit than the skins of other *Actinidia* species (F. R. Harker; I. C. Hallett; A. G. Seal; person. commun.) but the structural basis of this is as yet unknown. If a commercial cultivar with an easily removed fruit skin can be achieved, it is probably important that the hairs be either already shed or consistently persistent so that the fruit flesh is not contaminated with hairs.

4. Fruit Color. Chlorophylls, carotenoids, and anthocyanins are the most important pigments responsible for color in fruit. The fruit flesh of the best-known kiwifruit, *A. deliciosa*, is a brilliant, translucent emerald green (Plate 1.2B) which contrasts with the white core and the black seed. The fruit flesh is green because of the retention of chloroplasts and chlorophyll in the ripe fruit (Possingham et al. 1980; Hallett et al. 1995) and the fruit flesh of most other *Actinidia* species is likewise green when the fruit are mature and eating ripe (Huang et al. 2004). Most *Actinidia* fruit can therefore be classified as "stay-green" fruit: they are unusual in that unlike most other cultivated fruit, chlorophyll is not lost on ripening and the chloroplasts are not transformed into chromoplasts. The chlorophyll and carotenoid composition of the green fruit pericarp of *A. deliciosa* is similar to that of normal photosynthetically-active chloroplasts (Possingham et al. 1980; Ben-Arie et al. 1982; Fuke et al. 1985; Watanabe et al. 1986; Cano 1991; McGhie and Ainge 2002; Nishiyama et al. 2005). Chlorophylls and associated carotenoids have also been found at higher concentrations in the green-fleshed fruit of *A. arguta* (Plate 1.2A) and *A. rufa* (Nishiyama et al. 2005) although these concentrations are still much lower than in leaves. Fruit that appear deeper green to the eye have higher concentrations of chlorophyll (Nishiyama et al. 2005).

At eating ripeness, the fruit flesh of some cultivars of *A. chinensis* is still bright green, e.g., 'Wuzhi No. 3', but in most cultivars of this species the flesh color ranges from lime-green to a bright golden-yellow (Plate 1.2B or see Ferguson 1999a). The fruit flesh of such yellow-fleshed cultivars, e.g., 'Hort16A', is initially green during fruit growth and development (Minchin et al. 2003), and the change in color from green to varying shades of yellow has been ascribed to a gradual loss of chlorophyll during maturation, so that the yellow due to carotenoids is unmasked, without there being a concomitant increase in carotenoids (McGhie and Ainge 2002). The hue of the flesh when ripe depends to a large extent on the amount of chlorophyll retained: there is thus variation in the timing and the extent to which chlorophyll is degraded during ripening and storage, the extremes being yellow or green flesh at eating ripeness.

The fruit of *A. macrosperma* (Plate 1.1C), *A. polygama*, *A. tetramera*, and *A. valvata* change rapidly during maturation and ripening from bright green to a yellowish orange or bright orange (Montefiori et al. 2003). This change in color has likewise been ascribed to a loss of chlorophyll and extensive conversion of the chloroplasts to chromoplasts (McGhie and Ainge 2002). However, in at least *A. macrosperma*, the change in color is more than just a demasking of the yellow color of the carotenoids as the chlorophyll is lost: maturation is accompanied by an increase in carotenoids (Montefiori et al. 2004). The final color achieved depends on the particular carotenoids present indicating that it might be possible to select new cultivars whose flesh color varied from yellow through to bright orange (McGhie and Ainge 2002).

Anthocyanins, the third main group of fruit pigments, are important in some kiwifruit. Red flesh was first found in the fruit of *A. chinensis* from part of Hubei (Liang 1982b) and its presence has been used to distinguish the variety *A. chinensis* var. *rufopulpa* (C.F.Liang et R.H.Huang) C.F.Liang et A.R.Ferguson, although red pigments in the inner pericarp are also sporadically found in *A. chinensis* from Henan and other parts of China. A variant of *A. deliciosa* with red pigments in the inner pericarp, *A. deliciosa* var. *coloris* T.H.Lin et X.Y.Xiong appears to be restricted to the Dongshanfeng mountains in northern Hunan and southern Hubei (Lin and Xiong 1991). These genotypes of *A. chinensis* and *A. deliciosa* have a ring of bright red inner pericarp tissue surrounding the core (for illustrations, see Plates 1.1A and 1.2B, and Montefiori et al. 2005), with the intensity and distribution of the red pigments varying with genotype and with environmental conditions. In regions with warmer climates, the red flesh color is present during the early stages of fruit growth but fades by mid-summer when there is little difference between day and night temperatures (Huang et al. 2004). However the red color is more consistently expressed in regions with large diurnal changes in temperature, especially in the mountains at higher elevations. In *A. chinensis*, the main red pigments appear to be cyanidin 3-*O*-xylo(1-2)-galactoside followed by cyanidin galactoside, and in *A. deliciosa*, cyanidin glucoside followed by cyanidin galactoside (Montefiori et al. 2003, 2005). The first kiwifruit cultivar of *A. chinensis* with red flesh to be cultivated on a commercial scale is 'Hongyang' [Red Sun] (Huang and Ferguson 2003; Wang et al. 2003); a second cultivar 'Chuhong' was released recently (Wang et al. 2004).

Anthocyanins are probably responsible for the rather gloomy purple of ripe fruit of *A. arguta* var. *purpurea* (syn. *A. purpurea*) and the pink or red coloration in the fruit of some genotypes of other varieties of *A. arguta*, *A. henanensis*, and *A. melanandra* and of *A. arguta* × *A. melanandra* hybrids. Some of these fruit also change color as they ripen (Seager 1997) with *A. henanensis* (closely related to *A. arguta*) being unusual in that the core also becomes red on ripening (Cui et al. 2002). *Actinidia* fruit contain much lower concentrations of anthocyanins than many common berryfruit (Boyes et al. 1997; Montefiori et al. 2005).

Different combinations of chlorophylls, carotenoids, and anthocyanins can result in a wide range of fruit colors. Offspring produced by crossing *A. macrosperma* (fruit orange when ripe) with *A. melanandra* (fruit brick-red when ripe) have fruit with a spectacular range of colors when ripe (Plate 1.1D) from deep red, to orange, yellow, yellow-green to green. Different rootstock/scion interactions also appear to affect color expression (Boyes at al. 1997). There may be scope to modulate fruit color by choice of rootstocks and changes in vine management.

5. Ripening Indicators. The change in flesh color on maturation of yellow-fleshed cultivars such as 'Hort16A' can be important commercially, as mixed maturity can result in fruit whose internal color is inconsistent and ranges from lime-green through to the desired bright golden yellow. Such changes are not obvious unless the fruit is cut open. If, however, the fruit lack hairs and their skins are essentially transparent or the same color as the underlying flesh, changes in fruit color on maturation can serve as useful ripening indicators as well as being attractive. This occurs in some species of the *Leiocarpae* (Plate 1.1C). However, such color changes usually occur too late in fruit softening to indicate when fruit should be harvested (Hassall et al. 1998).

Furthermore, in those fruit that do change color on ripening, color development may be inhibited if the fruit are harvested mature, but green, and then stored. Thus, fruit from some *A. arguta* and *A. arguta* × *A. melanandra* crosses and backcrosses turn red as they ripen, but to ensure fully colored fruit, they must be harvested only after they are red or nearly completely red on the vine and are therefore soft with a very short storage life (Hassall et al. 1998).

6. Fruit Texture. *Actinidia* fruit consist of 4 zones, skin, outer pericarp, inner pericarp, and core, of which only the last 3 zones are usually eaten, although in some cases the skin can also be eaten. The relative proportions of these tissues can vary with genotype, especially in the ratio of the core to the pericarp diameter (Cotter et al. 1991; Huang et al. 2004). In a comprehensive study of 25 genotypes from 14 different *Actinidia* species, White et al. (2005) found that the softening of these 3 edible tissue zones during ripening followed much the same pattern as for the whole fruit. However, in some genotypes (*A. glaucophylla* and one genotype of *A. rufa*), the core did not soften even though the inner and outer pericarp had, and in 2 other genotypes (*A. chinensis* 'Wuzhi No. 2' and a different genotype of *A. rufa*) the core did soften but remained significantly firmer than the pericarp, even when the fruit were very ripe. Among *A. deliciosa* cultivars, the cores of "eating ripe" 'Gracie' fruit tend to be larger and remain harder (Cotter et al. 1991). Such differences can affect consumer acceptability.

The ripe fruit can range in texture from juicy (e.g., *A. chinensis*) to almost gelatinous (e.g., *A. arguta*), although individual genotypes within a species may also vary in texture, particularly flesh smoothness and flesh stringiness (Stec et al. 1989; Cotter et al. 1991; Jaeger et al. 2003). Although larger fruit (e.g., of *A. chinensis*, *A. deliciosa*, and *A. eriantha*) tend to be consistently softer when fully ripe than fruit from small-fruited species (White et al. 2005), the woody spike often found at the stalk end is usually found only in larger fruit, especially those of *A. chinensis* and *A. deliciosa*, and is particularly noticeable in cultivars such as *A. chinensis* 'Kuimi'. Hard cores or such woody spikes could rule out some selections as commercial cultivars.

7. Fruit Flavor. Most *Actinidia* fruit are edible even if only a few are really palatable (Ferguson 1990d). Individual genotypes of species such *A. arguta*, *A. callosa*, *A. chinensis*, *A. chrysantha*, *A. deliciosa*, *A. kolomikta*, and *A. hubeiensis* are described as having fruit with an excellent flavor; other genotypes of the same species have fruit that are bland and boring or mildly unpleasant. The unripe fruit of *A. polygama*, *A.*

macrosperma, and *A. valvata* are bitter and astringent with a mouth-numbing, shocking, peppery (chili) flavor, although this decreases as the fruit ripen.

In this discussion, we define flavor as being the sum of taste and odor (aroma) but recognize that fruit texture is also important, as are the chemical changes that occur when the fruit is chewed in the mouth (F. R. Harker, person. commun.). Flavors can change dramatically as fruit mature from under-ripe to over-ripe and the window of acceptability also varies according to genotype, with over-ripe fruit of some genotypes developing off-flavors, especially the so-called "vomit" flavors. The extensive literature on how factors such as dry matter content, maturity, storage, firmness when tested, length of storage, and even the temperature of storage of *A. deliciosa* 'Hayward' fruit can all affect flavor perceptions and preferences in just one cultivar (e.g., Stec et al. 1989; Jaeger et al. 2003; Marsh et al. 2004) indicates the difficulty of making meaningful comparisons of the flavors of fruit from different *Actinidia* species with the concomitant difficulties in comparing like with unlike. The analytical comparisons that have been made are largely confined to fruit of a restricted number of genotypes of *A. chinensis* and *A. deliciosa*: preference mapping indicates that most of the particular genotypes studied of *A. chinensis*, with sweeter flavors and overtones of black currant, aromatic melon, and candyfloss, are separated by consumers from genotypes of *A. deliciosa* which are more acid and less "fruity" (Esti et al. 1998; Jaeger et al. 2003; Wismer et al. 2005). However, the sensory profiles did not always segregate according to species, as fruit of one genotype of *A. chinensis* and of a hybrid between *A. chinensis* and *A. deliciosa* had flavor profiles that placed them with fruit of *A. deliciosa* genotypes. The most encouraging conclusion from such sensory studies for kiwifruit breeders is that the success of *A. chinensis* 'Hort16A' was not that it was preferred by all consumers to the existing *A. deliciosa* 'Hayward'—it wasn't—but because it had a new and distinct flavor profile that created a new product niche (Wismer et al. 2005). The diversity within the rest of the genus thus allows for many new breeding targets.

Many different flavor volatiles have been identified in *A. deliciosa* 'Hayward' kiwifruit with about 15 of these being considered more important (Young and Paterson 1990). The characteristic "kiwifruit" flavor seems to be associated mainly with ethyl butanoate, (*E*)-2-hexenal and some C6 alcohols (Gilbert et al. 1996; Jordán et al. 2002). The fruit of *A. arguta*, with their very distinct aroma notes, likewise produced complex mixtures of volatiles, particularly esters which have sweet "fruity" odors (Matich et al. 2003). Further work of this nature is required to determine the compounds responsible for the characteristic and distinctive flavors of different *Actinidia* genotypes and the changes that occur as the fruit are eaten.

Taste is largely determined by the relative concentrations of acids and sugars present. In *A. deliciosa* 'Hayward' kiwifruit, the main sugars are glucose, fructose, and sucrose, and the main organic acids are citric, quinic, malic, and ascorbic (Paterson et al. 1991). The various acids result in different perceptions of acidity, and ascorbic increases perceptions of acidity as well as other flavor components, whereas the various sugars appear not to differ in their effects on perceptions of sweetness (Marsh et al. 2003). Fruit of the different *Actinidia* species contain very different amounts of sugars and acids (Huang et al. 1983; Li et al. 1985; Chen et al. 1987; Huang et al. 2000b, 2004). Even within seedling populations of the one species (*A. chinensis*), there can be enormous variation in dry matter, soluble solids concentration, fruit flesh pH, and the concentrations of total acids, individual acids, and sugars. Many of these characters are highly heritable, indicating that they are amenable to selection (Cheng et al. 2005).

8. Health Constituents. The nutritional benefits of kiwifruit consumption have long been recognized and have played an important role in the commercial promotion of kiwifruit in the fresh fruit market (Ferguson and Ferguson 2003; Ferguson and Stanley 2003). Kiwifruit are a good source of minerals and of dietary fiber, and they contain a most effective laxative. Their outstanding nutritional quality is their very high content of vitamin C (ascorbate): their main disadvantage is that they induce allergic responses in some consumers. In China, the kiwifruit was formerly called king of the fruits because of its remarkably high vitamin C content.

Detailed and comprehensive nutritional data are available mostly for the fruit of *A. chinensis* 'Hort16A' and *A. deliciosa* 'Hayward' (Ferguson and Ferguson 2003) and some of the older *A. deliciosa* cultivars (e.g., Adorisio et al. 1990; Lintas et al. 1991). Although kiwifruit are a good source of minerals, especially potassium, any differences in mineral content are usually small and not likely to be important nutritionally (Samadi-Maybodi and Shariat 2003). Likewise, although there are very big differences among species in the concentrations of total soluble solids, total acids, and total sugars in the fruit and of individual sugars and acids (Huang et al. 2004), these differences are likely to be important in terms of taste, not nutrition. As far as human health is concerned the important changes are probably those in actinidin content, allergens, oxalate, and vitamin C.

Actinidin and Allergens. Kiwifruit contain large amounts of the highly active proteolytic enzyme actinidin (E.C. 3.4.22.14). At the levels of activity expressed in *A. deliciosa* 'Hayward' kiwifruit, actinidin does not seem to be a major health hazard for most people, but it can cause damage to the lips (especially at the corners of the mouth) although usually only if very large quantities of fruit are eaten. Peeling large numbers of fresh fruit can result in skin loss if hands are not protected.

Actinidin enzyme amounts and protease activities in the fruit can vary greatly among species and cultivars, e.g., compared with the levels in *A. deliciosa* 'Hayward', they are significantly higher in *A. chinensis* 'Kuimi', and *A. deliciosa* 'Abbott', and 'Koryoku' and much lower, at less than one tenth the total protease activity, in *A. chinensis* 'Hort16A' and 'Hongyang' (Nishiyama and Oota 2002; Nishiyama et al. 2004). Very low activities are also found in some selections of *A. polygama* and *A. rufa* and higher or much higher activities in various selections of *A. arguta* and *A. arguta* var. *purpurea* (Boyes et al. 1997; Nishiyama et al. 2004). Rootstock/scion interactions can also affect actinidin activities (Boyes et al. 1997).

Actinidin has been linked to "mouthburn" (mild irritation) (Boyes et al. 1997) and to the well-known laxative effect of kiwifruit. Large differences in actinidin content and activity could therefore influence consumer acceptability of different kiwifruit selections.

Much more important is the association of actinidin with allergic responses to kiwifruit. These have become more common with the commercialization and widespread distribution of kiwifruit (Lucas et al. 2003) and have recently been confirmed unambiguously by double-blind, placebo-controlled food challenge studies (Alemán et al. 2004). Actinidin is the major allergen in *A. deliciosa* 'Hayward', but other compounds are also involved, and although *A. chinensis* 'Hort16A' contains very little detectable actinidin, the presence of common allergens means that there is allergenic cross-reactivity between the two cultivars. People with an allergy to *A. deliciosa* 'Hayward' kiwifruit may therefore be equally susceptible to *A. chinensis* 'Hort16A' kiwifruit even if they have never before eaten them (Bublin et al. 2004). Allergenic cross-reactivity might well extend more generally to other *Actinidia* fruits.

Oxalate. The levels in *A. deliciosa* 'Hayward' (c. 25 mg total oxalate/100 g fresh weight [FW]) do not constitute a nutritional problem as some other common foods contain considerably more. However, most insoluble oxalate in kiwifruit occurs in the form of raphide crystals and these have been associated with irritation of the throat when processed kiwifruit products are eaten (Walker and Prescott 2003). The irritation is possibly aggravated by high levels of fruit acidity. Fruit of different *Actinidia* genotypes vary in their total oxalate contents: fruit of one genotype of *A. rufa* contained about the same as in 'Hayward', fruit of some *A. arguta* selections one quarter to one third this level, and fruit of a number of different genotypes of *A. chinensis* between one third and twice as much (Watanabe and Takahashi 1998; Rassam and Laing 2005). Raphide shape also varies: the raphides in *A. arguta*, *A. chinensis*, and *A. rufa* are about half the length of those in 'Hayward' and 'Bruno' (Watanabe and Takahashi 1998). Such variation in raphide crystal shape may have more effect on palatability than variation in total oxalate content.

Vitamin C. Vitamin C has received more attention than any other constituent of kiwifruit because it has long been recognized as the single most important nutrient. A typical *A. deliciosa* 'Hayward' kiwifruit contains about 85 mg ascorbate/100 g FW, a fruit of *A. chinensis* 'Hort16A' 30 to 40% more, about 105 to 110 mg ascorbate/100 g FW (Ferguson and MacRae 1992; Ferguson and Ferguson 2003). On a fresh weight basis, 'Hayward' kiwifruit contain 50% more vitamin C than an orange, five or six times as much as a banana or ten times as much as an apple. Only a few readily available fruit, such as blackcurrants, are richer in vitamin C. The USRDI (recommended daily intake) for vitamin C ranges from 30 mg for a child to 120 mg for a lactating mother. A single, average-sized 'Hayward' kiwifruit could by itself, therefore, provide the daily intake recommended for most of the population.

There is tremendous variation between species in ascorbate concentrations, from as low as 4 to 5 mg/100 g FW in fruit of *A. henryi* and *A. rudis* to the astonishing levels, enough to account for more than 1% of the fresh weight, in *A. latifolia* (671 to 2140 mg/100 g FW) and *A. eriantha* (500 to 1379 mg/100 g FW) (Huang et al. 2004). Fruit of *A. kolomikta* likewise contain remarkably high amounts of ascorbate, up to 1% fresh weight (Chesoniene et al. 2004). When fruit size is taken into account, the best sources of vitamin C in the genus are the fruit of *A. chinensis*, *A. deliciosa*, and especially *A. eriantha*.

The ranges of ascorbate contents quoted (Huang et al. 2004) indicate that there can also be considerable variation within taxa. Considering only *A. chinensis*: Huang et al. (2004) cite a range 50 to 420 mg ascorbate/100 g FW; ascorbate concentrations in fruit of 200 wild vines from Henan varied from 16.6 to 400 mg/100 g FW (Yin and Li 1982); in vines from Guangxi 20 to 180 mg/100 g FW (Li et al. 1985); in a population of 289 female vines arising from a factorial crossing of 3 females by 13 males, the family means for ascorbate content ranged from 21.4 to 238.1

mg/100 g FW (Cheng et al. 2005); and in 143 fruiting plants from a single cross from 48.6 to 208.9 mg/100 g FW (A. R. Ferguson unpubl.). Similarly, published values for ascorbate concentrations in fruit of *A. deliciosa* range from 30 to c. 400 mg/100 g FW (Ferguson 1990d), and in a population of 65 female vines of *A. eriantha* raised from the one collection of seed, the ascorbate content was 195 to 720 mg/100 g FW (Bank and Ferguson 1986).

Existing commercial kiwifruit cultivars outside of China were selected on attributes other than vitamin C content but show considerable variation. Fruit of 'Abbott' and 'Allison' contain the lowest ascorbate concentrations of any *A. deliciosa* cultivars, and 'Bruno', the highest, usually about 50% more than in 'Hayward'. Some of the more widely grown *A. chinensis* and *A. deliciosa* cultivars in China contain at least twice as much ascorbate as in 'Hayward' fruit (Cui et al. 2002; Nishiyama et al. 2004). However, even *Actinidia* cultivars with relatively low contents are very good sources of vitamin C.

Selection for high vitamin C in new cultivars should be feasible as, at least in *A. chinensis*, ascorbate content had a high heritability (Cheng et al. 2005). Fortunately, selection for increased soluble sugar content should lead to a simultaneous increase in ascorbate content (Cheng et al. 2005).

9. Other Fruit Characteristics. Other fruit characteristics such as time of maturity and ripening, handling and storage responses, and yield potential are discussed in Ferguson (1990d). Fruit of *A. chinensis* and *A. deliciosa* reach harvest maturity only after a particularly long growing season and there is an incentive to select for early maturity, especially for planting in districts that suffer early autumn frosts. The markedly superior storage life of *A. deliciosa* 'Hayward' fruit (Cotter et al. 1991) is one of the main reasons for the eventual reliance of the New Zealand kiwifruit industry on this cultivar. Storage life, as assessed by general fruit softening, by tissue breakdown, or by the development of off flavors, will remain an important criterion in the selection of new cultivars.

A separate issue is how fruit growth and composition in an individual genotype respond to different climatic conditions or different management regimes. *A. deliciosa* 'Hayward' seems reasonably tolerant of different climatic conditions and fruit of adequate quality are produced in many parts of the world. However, there appear to be no rigorous comparisons using measures of quality, such as flesh color, composition, flavor, or storage life of the fruit produced by 'Hayward' in different districts. Experimental manipulation of growing conditions indicate that in ‘Hayward’, high temperatures during summer would be expected to reduce fruit size and quality, whereas higher temperatures during autumn should increase fruit size and fruit dry matter content, but reduce vitamin C concentrations and delay the onset of maturity (Seager et al. 1996; Richardson et al. 2004; Snelgar et al. 2005). One might therefore predict differences in the fruit produced under different climatic conditions such as, for example, Italy versus New Zealand. Experience so far suggests that *A. chinensis* ‘Hort16A’ might be less tolerant than ‘Hayward’ of differences in growing conditions. Differences in adaptability to different conditions could be important, particularly with the trend for year-round supply of the fruit of cultivars such as ‘Hort16A’ and ‘Jintao’ being sought by growing vines in the opposing hemispheres. Fruit from different growing conditions may not necessarily be identical in fruit composition, quality, or behavior.

C. Gender Variation

Actinidia deliciosa and *A. polygama* are functionally dioecious (Brundell 1975; Schmid 1978; Ferguson 1984; McNeilage 1988, 1991a; Kawagoe and Suzuki 2004). Female plants produce morphologically perfect flowers with well-developed pistils and stamens (Plate 1.2D), but their stamens produce nonviable pollen; flowers of male plants have small, rudimentary ovaries (Plate 1.2C) without viable ovules but their stamens release viable pollen (Rizet 1945; Schmid 1978; White 1990). Pistil development in staminate flowers stops at an early stage (Brundell 1975; Schmid 1978; Polito and Grant 1984; Watanabe and Takahashi 1984) whereas pollen development in pistillate flowers stops at a very late stage of development (White 1990; Messina 1993; Scoccianti et al. 1999; Coimbra et al. 2004). This type of floral mimicry, in which unrewarding pistillate flowers mimic pollen-producing staminate flowers, is known as cryptic dioecy (Schmid 1978), and the stamens of pistillate flowers are important in attracting pollinating insects (Kawagoe and Suzuki 2004). All other *Actinidia* species appear to be functionally dioecious: all species have morphologically distinct staminate and pistillate flowers on separate vines; the male plants normally do not carry fruit and the female vines, when checked, normally do not produce viable pollen. It is likely that a common genetic mechanism operates to maintain dioecy in all species and that this mechanism evolved before speciation and before polyploidization (Harvey et al. 1997; Yan et al. 1997b). Commercial orchards of *A. arguta*, *A. chinensis*, and *A. deliciosa* have pollenizer (male) vines interplanted in a regular pattern among the fruiting (female) vines to ensure economic yields.

Variation in floral development or gender inconstancy was first noticed in New Zealand orchards of *A. deliciosa* (Ferguson 1984; Ferguson and Davison 1986) with the identification of "fruiting male" plants which produce both staminate flowers and flowers which are, to varying extents, bisexual (McNeilage 1991a,b). Since then, at least 6 different gender phenotypes have been identified: male, fruiting male, neuter, female, inconstant female, and hermaphrodite (McNeilage 1997). Flower morphology is not always a reliable indication of gender and to be certain, the ovary should be dissected to check for viable ovules and the viability of pollen should also be tested (McNeilage 1991a). Phenotypic gender expression seems to be a continuum, as inconstant male flowers vary within a vine in the number of viable ovules and even individual inflorescences can contain both bisexual and staminate flowers. There is also variation from year to year (Messina et al. 1990; McNeilage 1991b; Seal and McNeilage 1989). Experimental manipulation might affect sex expression. Some individual callus lines from endosperm tissue of *A. chinensis* gave rise to both male and female regenerated plants raising the intriguing possibility that, although many of the regenerants were aneuploid, it might be possible to produce male or female clones of a particular genotype (Gui et al. 1993).

Gender inconstancy is not restricted to *A. deliciosa* but has also been observed in *A. arguta* (Hirsch et al. 1990), *A. chinensis* (Tang and Jiang 1995), and *A. eriantha* (Cui et al. 2002), and would probably be found in other *Actinidia* species if enough plants were studied. Occasional monoecious plants have also been reported: several seedlings produced by crossing *A. chinensis* with *A. eriantha* were probably fruiting males in that they had both staminate flowers (producing viable pollen) and pistillate flowers (which could be set) on the same canes (Ke et al. 1992).

Karyotyping of *Actinidia* is very difficult because there are so many chromosomes ($x = 29$) and these are all so small (< 1 μm) (He et al. 2003, 2005; see also Section II.D). Nevertheless, He et al. (2003) were able to conclude that two nucleolar chromosomes in diploid male *A. chinensis* plants were unable to pair completely and that they therefore differed in their satellite regions. These sex chromosomes in *Actinidia* appear to be at an early stage of differentiation and the sex determination mechanism is probably of the X_nX/X_nY type, the male being heterogametic. Selfed fruiting males produce both male and female progeny, confirming that it is the male that is heterogametic (Testolin et al. 1995a). Such a sex determination mechanism is consistent with the disomic inheritance and the 1:1 male : female sex ratios observed in *Actinidia* in both controlled crosses and plants raised from seed collected in the wild and at different ploidy levels (McNeilage 1991a, 1997; Testolin et al. 1995a, 1999b; Harvey et al. 1997), i.e., XX = female and XY = male in diploids; XXXX = female and XXXY = male in tetraploids; XXXXXX = female and XXXXXY = male in hexaploids, etc. This type of sex-determining system is termed active-Y (Testolin et al. 1995a, 1999b, 2004; Harvey et al. 1997; McNeilage 1997) and probably involves at least two tightly-linked genes, one for pistil suppression, the other for pollen development. The situation is similar to that observed in other dioecious plants such as spinach, in which ploidy can be manipulated (Janick 1955; Janick and Stevenson 1955). The major sex-determination genes may interact with other genes influenced by the environment, as is found in grapes (Moore 1970). Maintenance of dioecy and 1:1 sex ratios at different ploidy levels (McNeilage and Ferguson 2006) is readily explained by assuming that in *Actinidia*, as in most other plants, sexual polyploidization through the production of numerically unreduced gametes has played an important role in the evolution of the genus (Testolin et al. 1995a; McNeilage 1997). Production of numerically unreduced gametes has been reported in *A. chinensis* (Yan et al. 1997b).

Manipulation of gender diversity in *Actinidia* has practical implications. Breeding in dioecious plants means that pollen parents are often selected “in the dark” as fruiting characteristics are not expressed in the male. Production of some viable pollen by a female plant enables breeders to select a pollen parent with a better understanding of fruit characters, although progeny testing provides much more convincing information. More useful would be the development of experimental procedures that would routinely encourage female plants to produce even some viable pollen as this would allow direct crossing of two selected female cultivars.

A fully hermaphrodite cultivar that is self-fertile and self-setting would have many economic advantages. At present, about 10 to 15% of the canopy in commercial orchards is occupied by nonfruiting male pollenizers which must coincide in flowering with the fruiting cultivars but have to be trained and pruned differently. Furthermore, many aspects of orchard management are designed to keep bees brought into the orchard active and effective in transferring pollen from the pollenizer plants to the fruiting plants. Self-fertile, completely hermaphroditic plants, carrying only bisexual flowers, have been obtained from crosses between *A. deliciosa* ‘Hayward’ and an inconstant (fruiting) male (McNeilage and Steinhagen 1998), from crosses in which an hermaphrodite was one of the parents, or when an hermaphrodite was selfed (McNeilage 1997). Hermaphrodites are morphologically indistinguishable from females except in having fertile pollen and are therefore considered to be phenotypically altered females. The fruit of these plants so far preclude their use as commercial cultivars. They show, however, that suitable hermaphrodite cultivars of *A. delicosa* and, possibly, other *Actinidia* species should be achievable. It is therefore important to identify and conserve gender variants when they occur.

D. Ploidy Variation

1. Basic Chromosome Number. *Actinidia* is unusual in the extent of intertaxal and intrataxal variation in ploidy: of 50 *Actinidia* taxa studied so far, chromosome counts and flow cytometry measurements have revealed that 40 taxa contain diploids, 20 taxa tetraploids, 5 taxa hexaploids, and 1 taxon contains octoploids (Table 1.4). A distinctive feature of the genus is the structured reticulate pattern of diploids, tetraploids, hexaploids, and octoploids in diminishing frequency, associated, in at least some taxa, with geographic separation of ploidy races (Xiong 1992; Yan et al. 1994; Ferguson et al. 1997). Such a reticulate polyploid superstructure above a broad diploid base has been found in other genera (Swaminathan 1970), as has also a greater frequency of tetraploids than other polyploids (de Wet 1980). Even the occasional dodecaploid has been raised from seed collected from fruit of wild *A. deliciosa* plants (A. R. Ferguson unpubl.) although it is not certain that such plants would survive outside of cultivation.

The somatic chromosome counts by Xiong et al. (1985), McNeilage and Considine (1989), and Yan (1996) of more than 100 genotypes at different ploidy levels (2*x*, 3*x*, 4*x*, 5*x*, and 6*x*) convincingly established that in *Actinidia* the basic chromosome number is 29. Furthermore, at diakinesis and metaphase I of meiosis, diploids had 29 bivalents; tetraploids, mainly 58, and hexaploids, mainly 87 with few polyvalents (Lu et al. 1984; McNeilage and Considine 1989; Xiong et al. 1993; Yan 1996). This basic chromosome number has been confirmed by all subsequent counts. It is possible that such a high basic number is itself polyploid in origin, as has been suggested for other angiosperm genera with high basic chromosome numbers (Stebbins 1971). Thus, ancestral *Actinidia* species may have had a basic chromosome number of $x = 14$ and/or $x = 15$ and during evolution, chromosome duplication may have occurred, preceded, or followed by at least one aneuploid event (McNeilage and Considine 1989), such as the breakage of a centromere to add one new chromosome (He et al. 2005). Chromosome duplication is also indicated by about 20% of primer pairs for microsatellites being apparently amplified at two distinct loci (Huang et al. 1998; Testolin et al. 1999c), although other possibilities should also be considered (Testolin et al. 2001). Allozyme polyallelism suggested that 10 *Actinidia* taxa, at that

Table 1.4. Diversity of ploidy in the genus *Actinidia*. Ploidy estimates denoted by f.c. are based on flow cytometry, all other estimates are chromosome counts.

Taxon	Chromosome number	Ploidy	References
A. arguta var. *arguta*		2*x* (f.c.)	*y*
		2*x*	*p,d,b*
		4*x* (f.c.)	*y,v,j,i,e*
		4*x*	*g*
		4*x*	*f*
		4*x*	*z*
		4*x*	*x,w,r,q,p,m,d,b,ww,uu,ss*
		6*x* (f.c.)	*y,v,i*
		6*x*	*d,b,uu,ss*
		7*x*	*i*
A. arguta var. *purpurea*		4*x* (f.c.)	*y,v,p,j,e*
	116	4*x*	*r,q*
		8*x* (f.c.)	*v*
	ca. 232	8*x*	*uu,tt*
A. arisanensis		2*x* (f.c.)	*y*
	58	2*x*	*r,q*
A. callosa var. *discolor*	58	2*x*	*r,q,p,rr*
	116	4*x*	*r,q,p,yy*
A. callosa var. *henryi*		2*x* (f.c.)	*v*
	58	2*x*	*r,q,p,m*
		4*x* (f.c.)	*u*
	116	4*x*	*r,q,p,yy*
A. callosa var. *formosana*		2*x* (f.c.)	*y*
A. callosa var. *strigillosa*	116	4*x*	*r,q,p*
A. chinensis var. *chinensis*		2*x* (f.c.)	*y,v,l*
	58	2*x*	*v,s,r,q,p,o,k,zz,ss,qq,pp,oo,nn*
		4*x* (f.c.)	*v,l,e*
	116	4*x*	*x,r,q,p,a,zz,xx,vv,uu,tt,ss*
A. chrysantha		4*x* (f.c.)	*v,l*
	116	4*x*	*r,q,p,yy,uu,ss*
A. cylindrica var. *cylindrica*	58	2*x*	*r,q,p,yy*
A. cylindrica var. *reticulata*	58	2*x*	*r,q,p*
	116	4*x*	*r,q,p*
A. deliciosa var. *deliciosa*	116	4*x*	*x*
		6*x* (f.c.)	*y,v,l,j,i,e*

(*continued*)

Table 1.4. (*continued*)

Taxon	Chromosome number	Ploidy	References
	160	6*x*	*h*
	ca. 170	6*x*	*t,qq*
	174	6*x*	*r,q,p,m,d,b,uu,ss,oo,nn*
A. deliciosa var. *chlorocarpa*	116	4*x*	*s,r,q,p*
		6*x* (f.c.)	*v*
	?174	6*x*?	*p,uu,ss*
A. deliciosa var. *coloris*		6*x* (f.c.)	*v*
	174	6*x*	*uu,ss*
A. eriantha var. *eriantha*		2*x* (f.c.)	*y,v,l,j*
	58	2*x*	*w,r,q,p,n,m,a,ww,uu,ss,pp*
A. eriantha f. *alba*	58	2*x*	*r,q,p*
A. eriantha var. *brunnea*		2*x* (f.c.)	*v*
	58	2*x*	*r,q,p,ss*
A. eriantha var. *calvescens*	58	2*x*	*r,q,p*
A. farinosa	58	2*x*	*p*
A. fulvicoma var. *fulvicoma*	58	2*x*	*s,r,q,p*
A. fulvicoma var. *lanata*		2*x* (f.c.)	*v*
	58	2*x*	*r,q,p,yy*
A. glaucophylla var. *glaucophylla*		2*x* (f.c.)	*v*
	58	2*x*	*r,q,p,uu,ss*
A. glaucophylla var. *asymmetrica*	116	4*x*	*r,q,p*
A. grandiflora	58	2*x*	*r,q,p*
	116	4*x*	*s,v,q,p*
A. guilinensis		2*x* (f.c.)	*v*
	58	2*x*	*r,q,p,uu,ss*
A. hemsleyana var. *hemsleyana*		2*x* (f.c.)	*y*
	58	2*x*	*r,q,p,yy*
A. hubeiensis	58	2*x*	*s,r,q,p*
A. hypoleuca		2*x* (f.c.)	*v,i*
	58	2*x*	*r,q,m,uu,ss*
A. indochinensis		2*x* (f.c.)	*v*
	58	2*x*	*r,q,p,ss*
	116	4*x*	*r,q,p*
A. kolomikta		2*x* (f.c.)	*y,v,i,e*

Taxon	Chromosome number	Ploidy	References
	48	2*x*	*g*
	58	2*x*	*s,r,q,p,m,yy*
	c. 112	4*x*	*l*
	116	4*x*	*r,q,p,yy*
A. lanceolata		2*x* (f.c.)	*l*
	58	2*x*	*r,q,p,yy*
A. latifolia var. *latifolia*		2*x* (f.c.)	*v,l*
	58	2*x*	*w,s,r,q,p,yy,uu*
A. liangguangensis	58	2*x*	*r,q,p*
A. lijiangensis	58	2*x*	*r,q,p*
A. macrosperma var. *macrosperma*		4*x* (f.c.)	*v*
	116	4*x*	*w,p,yy,ss,rr*
A. macrosperma var. *mumoides*	116	4*x*	*r,q,p*
A. melanandra var. *melanandra*		2*x* (f.c.)	*v*
	58	2*x*	*r,q,p,uu,ss*
		4*x* (f.c.)	*y,v,e*
	116	4*x*	*r,q,p,m,uu,ss*
A. melliana	58	2*x*	*r,q,p,yy*
A. persicina	58	2*x*	*r,q,p*
A. polygama		2*x* (f.c.)	*y,v,l,j,e*
	48	2*x*	*g*
	58	2*x*	*z,r,q,p,m,k,c,b,yy,uu,ss,rr*
	116	4*x*	*x,r,q,p,yy*
A. rubrucaulis var. *rubricaulis*	58	2*x*	*r,q,p,rr*
	96	4*x*	*g*
	116	4*x*	*r,q,p*
A. rubricaulis var. *coriacea*	58	2*x*	*r,q,p*
A. rufa		2*x* (f.c.)	*y,v,l,i*
	58	2*x*	*r,q,p,m,ss*
A. rufotricha var. *glomerata*	58	2*x*	*r,q,p*
A. sabiifolia	58	2*x*	*r,q,p,yy*
	116	4*x*	*r,q,p*
A. setosa		2*x* (f.c.)	*y,v*
	58	2*x*	*r,q,p,uu,ss*
A. styracifolia	58	2*x*	*r,q,p*
A. tetramera	58	2*x*	*q,p,o,nn*

(*continues*)

Table 1.4. (*continued*)

Taxon	Chromosome number	Ploidy	References
A. valvata var. *valvata*		4*x* (f.c.)	[v]
	116	4*x*	[r,q,p,uu,ss]
	174	6*x*	[r,q,p,o]
A. zhejiangensis	58	2*x*	[s,r,q,p]

[z]Baranec and Murin (2003), [y]Blanchet et al. (1992), [x]Bowden (1945), [w]Deng and Sen (1986), [v]Ferguson et al. (1997), [u]A.R. Ferguson unpubl., [t]Fraser and Harvey (1986), [s]He et al. (1998), [r]Huang et al. (2000b), [q]Huang et al. (2003), [p]Huang et al. (2004), [o]Li et al. (1988), [n]Lu et al. (1984), [m]McNeilage and Considine 1989, [l]M. A. McNeilage and A. R. Ferguson unpubl. (2006), [k]Nakajima (1942), [j]Ollitrault-Sammarcelli et al. (1994), [i]Phivnil et al. (2005), [h]Rizet (1945), [g]Shashkin quoted in Poyarkova (1949), [f]Sokolovskaya et al. (1989), [e]Start et al. (1997), [d]Suezawa (1989), [c]Tanaka et al. (1997), [b]Watanabe et al. (1990), [a]Xiong (1990), [zz]Xiong (1992), [yy]Xiong and Huang (1988), [xx]Xiong et al. (1993), [ww]Xiong et al. (1985), [vv]Xiong et al. (1998), [uu]Yan (1996), [tt]Yan et al. (1994), [ss]Yan et al. (1997c), [rr]Yao and Cui (1988), [qq]Zhang and Beuzenberg (1983), [pp]Zhang et al. (1997), [oo]Zhang (1983), [nn]Zhu (1982).

stage not checked for ploidy, might be polyploid (Huang et al. 1997): subsequent analysis has shown that 7 of these have so far proved to be solely diploid, further possible evidence of ancient chromosome duplication. In *Actinidia*, polyallelism is consequently not a reliable indication of polyploidy. *Actinidia* species could therefore be described as cryptic polyploids or rediploidized palaeopolyploids (Grant 1963; Goldblatt 1980).

Chromosomes in *Actinidia* are small and numerous (an octoploid contains 232 chromosomes) and accurate counts are both difficult and tedious. This is probably the reason for some earlier counts producing numbers that are not simply multiples of the basic number of 29 (e.g., Shashkin, cited in Poyarkova 1949).

Misidentification of taxa can also be a problem. During the early 20th century, *A. arguta* and *A. polygama* in European and North American collections were often confused and this type of error could account for some apparent anomalies. The plant supplied to McNeilage and Considine (1989) as *A. arguta* var. *giraldii* and shown to be diploid is now thought instead to be *A. hypoleuca*, a species sometimes treated as a variety of *A. arguta* (e.g., Phivnil et al. 2005). The plants studied by Yan et al. (1997c) of what was thought to be *A. deliciosa* var. *chlorocarpa* appear now to be not true to type—the alternative count of 116 for plants of this taxon (He et al. 1998), together with the morphological characteristics, suggest that it may be a hybrid between *A. chinensis* and *A. deliciosa*.

For most *Actinidia* taxa, chromosome counts have been determined for only 1 or 2 genotypes and the plants studied may not necessarily be typical or they may have come from only one part of an extensive geographic distribution. Furthermore, as discussed above, it is often difficult to identify individual genotypes, especially male plants. When chromosome counts are used to determine ploidy, *A. chinensis* is the only taxon to have been studied in convincing detail: Xiong (1992) counted at least 13 different genotypes, all tetraploid and Yan (1996) more than 60 genotypes, both diploids and tetraploids from nearly 40 different accessions. The next most studied taxon is *A. deliciosa* var. *deliciosa*: Yan (1996) counted 14 distinct genotypes of *A. deliciosa* (all hexaploid), although 6 of these were derived from the original introduction into New Zealand in 1904. Many of the published counts for *A. deliciosa* var. *deliciosa* are likewise of 'Hayward' or other New Zealand cultivars descended from the same accession.

2. Ploidy Races. Intrataxon ploidy variation has so far been observed in 15 *Actinidia* taxa (Table 1.4). Diploid and tetraploid races have been detected in 12 taxa, tetraploid and hexaploid races in 2 taxa (*A. valvata* var. *valvata* and *A. arguta* var. *arguta*). The conclusion that *A. deliciosa* var. *chlorocarpa* contains tetraploid and hexaploid races may be incorrect if the plant studied by Yan et al. (1997c) is not true to type. Once again, *A. chinensis* is the only taxon in which intrataxon ploidy races have been studied at all adequately. The first reported count for *A. chinensis* was 116 (Bowden 1945): the original provenance of the plant used was not given, but the illustration of the chromosome spread seems convincing and the plant studied may therefore have been tetraploid *A. chinensis*, not *A. deliciosa* as has often been assumed. Subsequent counts for *A. chinensis* all suggested that it was diploid ($2n = 2x = 58$) (Zhang 1983; Zhang and Beuzenberg 1983; Xiong et al. 1985; Deng and Sen 1986; McNeilage and Considine 1989). The first unequivocal report of tetraploid races of *A. chinensis* was that of Xiong (1992) who studied large-fruited selections from the Mufu and Wuling mountains of southeast Hubei and north Jiangxi. His work was extended by Yan et al. (1994) and Yan (1996) who counted 63 genotypes from 36 accessions of *A. chinensis*: 36 genotypes from 21 accessions were diploid and 27 genotypes from 15 accessions were tetraploid. This proportion of tetraploids may be considerably higher than that occurring naturally as all the large-fruited selections checked by Xiong were tetraploid and many of the plants studied by Yan were likewise large-fruited selections introduced because of their large fruit. The results suggest that tetraploid *A. chinensis* may be restricted to the mountainous regions of southeast Hubei, north Jiangxi, and north Fujian (Yan et al. 1994). Geographic localization of ploidy races in *Actinidia* is consistent with the behavior of other plants (Stebbins 1950).

There are few obvious morphological differences between diploid and tetraploid forms of *A. chinensis*. Diploid races flower about 2 weeks earlier than tetraploid races when grown at the one site, but this may simply reflect different geographic origins. Huang et al. (1997), however, suggest a positive correlation between ploidy level and fruit size.

There is good evidence of tetraploid and hexaploid races in *A. arguta* var. *arguta* (Suezawa 1989; Watanabe et al. 1990; Yan et al. 1997c) and if *A. hypoleuca* is treated as a variety of *A. arguta*, as is sometimes the case, and *A. arguta* var. *purpurea* (sometimes treated as a separate species) is also taken into account, then the species *A. arguta* would contain diploid, tetraploid, hexaploid, and octoploid chromosome races. Likewise, taxonomic judgements can affect the number of chromosome races in other taxa. For example, in the *A. chinensis*/*A. deliciosa*/*A. setosa* complex, formerly all considered as being within a single species, there are diploid, tetraploid, and hexaploid chromosome races. When Liang and Ferguson (1984) raised the then varieties *chinensis* and *deliciosa* (syn. *hispida*) of *A. chinensis* to specific status, the difference in ploidy was one of the characteristics considered. At that stage, it was thought that *A. chinensis* was always diploid and *A. deliciosa* always hexaploid but the discovery of ploidy races in *A. chinensis* and possibly *A. deliciosa* makes the distinction less clear cut. That so many *Actinidia* taxa have proved to have ploidy races when so few counts have been made for most taxa suggests that in individual *Actinidia* taxa, ploidy races are likely to be the rule rather than the exception. It is, therefore, unwise to make assumptions about the ploidy of any *Actinidia* plant collected from the wild. All that can be done is to determine the ploidy of a particular genotype or the likely ploidy of seedlings arising from a single collection of seed.

3. Nuclear DNA Content and Flow Cytometry. The tedium of counting large numbers of very small chromosomes has encouraged the search for other methods of determining ploidy in *Actinidia*. One possibility is to count the number of nucleoli, as diploid plants of *A. arguta* have 2 nucleoli, tetraploid plants of the same species, 4 nucleoli, and hexaploid *A. deliciosa* 6 nucleoli (Watanabe et al. 1990). Stomatal length has also been used to distinguish between trihaploid and hexaploid plants of *A. deliciosa* (Przywara et al. 1998) although subsequent authors (Fraser et al. 1992; Chat et al. 1996) have found the method unreliable for other than checking ploidy levels of a single genotype being treated with antimitotic agents

Flow cytometry is now the obvious choice (Blanchet et al. 1992; Hopping 1994a; Ollitrault-Sammarcelli et al. 1994; Ferguson et al. 1997; Start et al. 1997; M. A. McNeilage and A. R. Ferguson unpubl.) even if precautions have to be taken (Hopping 1993, 1994b). Flow cytometry allows much greater numbers of plants to be routinely studied. Start et al. (1997) were able to measure ploidy in 61 *Actinidia* genotypes, while M. A. McNeilage and A. R. Ferguson (unpubl.) checked ploidy in 746 genotypes. A. R. Ferguson (unpubl.) has estimated ploidy in approximately 2000 more genotypes in the HortResearch, New Zealand *Actinidia* germplasm collections as well as several thousand plants from breeding populations. Although chromosome counts are still necessary to verify ploidy, flow cytometry allows many individual seedlings from each of many different accessions of seed to be checked. For example, 53 genotypes from 26 accessions of *A. arguta* var. *arguta* proved to be tetraploid, whereas 2 accessions of bud wood of *A. arguta* var. *arguta* 'Issai' were both hexaploid; 20 plants from 4 accessions of *A. arguta* var. *purpurea* were tetraploid whereas 40 plants from three accessions of the same taxon were octoploid; 443 plants from 57 accessions of *A. chinensis* were diploid, and 180 plants from 34 accessions were tetraploid (A. R. Ferguson unpubl.). Such numbers leave no doubt as to the reality of ploidy races in at least some *Actinidia* taxa.

Determination of ploidy races within a taxon or of the ploidy of interspecific crosses in *Actinidia* by flow cytometry is possible because the DNA content of the 2C-nucleus does not vary greatly among different taxa (Blanchet et al. 1992; Ferguson et al. 1997) and because the amount of DNA in the nucleus is directly proportional to the ploidy (Ferguson et al. 1997). Thus, the average DNA content of the chromosome set does not decrease as the number of sets within the nucleus increases.

Ploidy can be determined by measurements of *relative* nuclear DNA content, using as controls, *Actinidia* plants of known chromosome number. Flow cytometry has also been used to estimate the *absolute* amount of DNA in the nucleus. Hopping (1993, 1994a) estimated that the 2C-value (as defined by Greilhuber et al. 2005) for *A. deliciosa* (hexaploid) was 4.2 to 4.5 pg DNA, which would correspond to about 4.2×10^9 bp (1 pg DNA = 0.978×10^9 bp, Doležel and Bartoš 2005). Ollitrault-Samarcelli et al. (1994) and Ferguson et al. (1997) obtained slightly lower 2C-values for *A. deliciosa* of 3.97 pg and 3.93 pg DNA/2C-nucleus respectively, which agree reasonably well with the estimate by Matsunaga et al. (1996) of about 3.5×10^9 bp. This is also consistent with the conclusion of Weising et al. (1996) that the 1C-value for diploid *A. chinensis* was 0.375 to 0.750×10^9 bp (equivalent to a 2C-value of 2.25 to 4.50×10^9 bp for *A. deliciosa*). Using Feulgen staining Lindsay (1995) got a somewhat higher figure of 5.58 to 7.96 pg/2C-nucleus, which corresponds to about 5.45 to 7.78×10^9 bp. Further measurements using accepted plant standards are necessary.

4. Consequences of Ploidy Variation for Kiwifruit Breeding. Ploidy variation between taxa and the existence of ploidy races within taxa can make crossing in *Actinidia* difficult. Before the full extent of this variation was realized, breeders did not understand why some crosses were so difficult or even impossible, e.g., why when two genotypes of *A. chinensis* were crossed, the success rate might be lower than when two different species such as *A. chinensis* and *A. eriantha* were crossed (Wang et al. 1989, 1994; Xiong 1990). We now know that whereas *A. eriantha* appears consistently to be diploid, there are diploid and tetraploid races of *A. chinensis* and success in crossing will partly depend on which particular ploidy level is used. It is, therefore, sensible to check the ploidy of any individual genotypes being used in crossing programs. The ploidy of offspring should also be checked because they are not always at the expected ploidy, especially when they result from interploidy crosses.

Ploidy variation does, however, provide kiwifruit breeders with new opportunities, in that creation of parents at different ploidy levels or of novel breeding lines or even of novel cultivars of different ploidies is now becoming possible as a result of easier methods for determining ploidy and a better understanding of what is involved. Use of embryo rescue techniques (Mu et al. 1990, 1992) might allow production from interploidy crosses of a continuous range in ploidy from diploid to above octoploid. Even dodecaploids have been reported, as somaclones arising from leaf-derived callus tissue cultures of *A. deliciosa* (Boase and Hopping 1995) or appearing as seedlings in accessions of *A. deliciosa* from the wild (A. R. Ferguson, unpubl.). Trihaploids of *A. deliciosa* have resulted from induced parthenogenesis stimulated by use of lethally irradiated pollen (Pandey et al. 1990; Chalak and Legave 1997) and dihaploids, possibly even haploids, could presumably be produced in the same way starting with genotypes at the appropriate ploidy level. Conversely, induced doubling of ploidy by antimitotic agents (e.g., Chalak and Legave 1996) could allow new opportunities in interspecific crossing or might increase fruit size in genotypes having fruit with otherwise good characteristics but inadequate size. Doubling of haploids could provide useful information on recessive characters and the inheritance of desirable characters. Interploidy crosses might also be facilitated by taking advantage of the production of numerically unreduced gametes, as has been observed in *A. chinensis* (Yan et al. 1997b). A better understanding of autopolyploidy vs. allopolyploidy in tetraploid *A. chinensis* and in *A. deliciosa*, and of tetrasomic gametic segregation in tetraploid *A. chinensis* might also assist in the design of kiwifruit breeding programs.

E. Molecular Heterozygosity

In kiwifruit there is considerable genetic variation in numerous characters (Zhu 1990; McNeilage 1991a; Beatson 1992; Blanchet and Chartier 1992; Testolin et al. 1995b; Zhu et al. 2002; Cheng et al. 2005) even though many of the plants studied have a common origin in the first introduction of seed to New Zealand. This heterozygosity despite such a narrow genetic base is probably due, at least in part, to the obligate outcrossing because of dioecy, and to polyploidy and the high chromosome number allowing extensive recombination.

Molecular analyses have also revealed that *Actinidia* is remarkably heterozygous. The genetic diversity at the isozyme level is extraordinarily high in both cultivars selected from the wild and in random representatives of different taxa (Messina et al. 1991; Huang et al. 1997; Testolin and Ferguson 1997; Huang et al. 2004). For example, in 22 cultivars of *A. chinensis* and *A. deliciosa*, the isozymic heterozygosity of 10 isozyme loci averaged 65% and in the limited numbers studied from each taxon ranged from 68% to 100%. Many of the loci studied were also multi-allelic, e.g., at the PGI (phopsphoglucose isomerase) locus, 55% of the plants were di-allelic, 27% tri-allelelic, and 18% tetra-allelic (Huang et al. 1997). The high rates of poly-allelism found in hexaploid *A. deliciosa* and tetraploid *A. chinensis* indicate effective maintenance of heterozygosity through polyploidy in *Actinidia* (Stebbins 1950). Some of the heterozygosity observed may be due to *Actinidia* species being cryptic polyploids or rediploidized palaeopolyploids (see Section II.D.1). The higher rates of tri- and tetra-allelic heterozygosity observed in selected cultivars, as compared with individual plants randomly collected from the wild, suggests that genetic heterozygosity should be an important objective in future breeding programs, particularly when mass or recurrent selection procedures are used (Ferguson et al. 1996).

Much of the recent molecular work with *Actinidia* is summarized in Xu et al. (2003) and Oliveira and Fraser (2005). Genetic diversity at the DNA level has not been studied in great detail but the results available indicate that both the nuclear and cytoplasmic genomes of *Actinidia* are very diverse, although, as in other species, chloroplastic DNA is more variable than mitochondrial DNA (Cipriani et al. 2003).

The extent of the diversity was revealed by analysis of RAPDs using 40 *Actinidia* taxa: although only 3 to 5 plants were examined for each taxon, 92% of the loci across taxa were polymorphic (Huang et al. 2002a). Microsatellites reveal even more diversity. Microsatellite heterozygosity ranging from 0 to 100% was found in 8 diploid *A. chinensis* accessions using 16 microsatellite DNA markers (Weising et al. 1996), as was considerable variability of microsatellites across different species. All 20 microsatellites examined by Huang et al. (1998) in 4 diploid and 6 tetraploid genotypes of *A. chinensis* were polymorphic with most having a very large number of alleles, from 9 to 17 per locus, with an average of 12.4 alleles per locus. The diploid genotypes showed a heterozygosity of 50 to 85%, the tetraploids 90 to 100%. The intralocus heterozygosity revealed by microsatellites in tetraploids was higher than that revealed by isozymes. Even greater diversity was found by Zhen et al. (2004) who used 9 microsatellite markers to examine 47 kiwifruit cultivars and selections of *A. chinensis* and *A. deliciosa*. The least variable microsatellite had 8 alleles, the most variable 38 alleles, the average was 23.7 alleles per locus. This is considerably higher than in most other woody plants studied as is the mean gene diversity. When the mean number of alleles per locus, the percentage of polymorphic loci and the direct count heterozygosity for each selection were calculated, *A. deliciosa* genotypes (hexaploid) were more variable than tetraploid *A. chinensis* genotypes which were, in turn, more variable than diploid *A. chinensis* genotypes. Again, the conclusion is that polyploidy has helped maintain genetic diversity in *Actindia* taxa. Apart from two selections from the same wild vine, all cultivars or selections could be uniquely identified by a single locus. Microsatellites are therefore more strongly discriminating than the polymorphic RAPD primers previously used, albeit on less diverse plants (Cipriani et al. 1997).

III. NATURAL DISTRIBUTION OF *ACTINIDIA*

A. Geographic Distribution of Commercially Important Species

Large quantities of fruit are harvested from wild *Actinidia* species in China. In the more eastern and southern provinces such as Jiangxi, Henan, Anhui, Zheijiang, and Yunnan, most of this fruit is of *A. chi-*

nensis. In more inland provinces such as Hubei, Sichuan, Shaanxi, and Hunan, the fruit is a mixture of the two species, *A. chinensis* and *A. deliciosa*, or predominantly of *A. deliciosa*. In subtropical provinces such as Guangxi, other species, such as *A. eriantha*, *A. latifolia*, and *A. indochinensis*, become more important. In the cold northerly provinces of Shandong, Liaoning, Jilin, and Heilongjiang, almost all the fruit collected is of *A. arguta*.

The natural distributions of *A. chinensis* and *A. deliciosa*, the two species of greatest commercial importance in terms of quantities of fruit collected from the wild and of cultivation, have been summarized by Ferguson (1990b) and Huang and Ferguson (2001), largely based on an analysis of herbarium records by Liang (1975). The species are widely distributed throughout China and, except for those provinces north of the Huang He, occur in most regions where any *Actinidia* are found (Lee 1990). *A. chinensis* grows mainly to the east and along the coast, south of the Huai He (Huai River) in eastern Henan, Anhui, Hubei, Hunan, Jiangxi, Fujian, and Guangdong (for map of provinces see Fig. 1.1); *A. deliciosa* grows more inland in colder regions as far north as the Qin Ling Mountains and to the west in Sichuan, Shaanxi, western Henan, western Hubei, western Hunan, Guizhou, Guangxi, and Yunnan. Where the two species overlap, as in southwestern Shaanxi, southwestern Henan, western Hubei, and western Hunan, they are usually separated vertically with *A. deliciosa* being found at higher, colder altitudes. Thus *A. chinensis* occurs mostly at altitudes between 200 and 900 m, but can be found as high as 1200 m (Li et al. 1985); *A. deliciosa* is usually at 800 to 1400 m, sometimes up to 1950 m. *A. chinensis* grows mainly in areas with annual rainfall 1000 to 2000 mm and 75 to 85% relative humidity, *A. deliciosa*, at annual rainfall of 600 to 1600 mm, and 60 to 80% relative humidity.

There may be some introgression between the two species (Liang 1975; Cui 1993). Thus, in the west of the Xuefeng Shan Mountains and the southeast of the Wuling Mountains of western Hunan, an area in which both *A. chinensis* and *A. deliciosa* occur, but *A. chinensis* predominates, *A. deliciosa* fruit have only short, sparse hairs and the fruit skin is relatively smooth. In the northwestern part of the Wuling Mountains, however, where both *A. chinensis* and *A. deliciosa* occur but *A. deliciosa* predominates, *A. deliciosa* fruit have rough skins with long hairs. The closely related species, *A. setosa*, originally included in *A. chinensis* s.l., appears to be restricted to Taiwan (see also Section II.A.5).

Actinidia chinensis and *A. deliciosa* are most common on mountain slopes in relatively damp, shady or semi-shady areas in gullies, especially along streams, under the tree canopy, or on the edge of the forest, or in clearings in mixed evergreen-deciduous forests. They are seldom found on the tops of hills where there is no shade and little moisture, or where there is exposure to strong winds. However, the two species seem robust and are often common in areas that have been cut over and are now regenerating. They can scramble along the ground but climb trees wherever possible, usually fruiting only when exposed to the light (Gao and Xie 1990). Climbing is assisted by the more vigorous shoots twisting tightly round supports and by the interlacing of the shorter shoots. *A. deliciosa* is surprisingly adaptable to different temperatures: it can tolerate high temperatures, e.g., 40°C in Wulong, Sichuan or very low winter temperatures, e.g., –20.4°C in Butao, Sichuan, although such tolerance depends on the stage of growth and development.

Actinidia eriantha also has some commercial potential because the fruit are large, at best usually about 50 g, and contain particularly high concentrations of vitamin C, up to 10 times those in *A. deliciosa* 'Hayward' kiwifruit (see Section II.B.8). Although some genotypes are reported to have sweet fruit, the fruit of most of this species do not have a particularly good flavor and the fruit skin is covered by copious amounts of long white fur, usually persistent until maturity. *A. eriantha* is similar, morphologically, to *A. chinensis* and *A. deliciosa*. It is a vigorous, robust vine and it is found widely throughout south China, south of the Yangzi River with a distribution both geographically and in altitude, similar to that of *A. chinensis*. However, it does not grow as far north or as far west but is found farther to the south. Thus, it does not occur in Anhui, Henan, or Hubei, and in Hunan it is restricted to southeastern and southwestern regions, whereas *A. chinensis* is much more widespread. *A. eriantha* is particularly widespread in Fujian, where about 1500 t of fruit are collected each year, and it extends farther south into Guangdong than does *A. chinensis* (Cui 1993).

Actinidia kolomikta has very sweet fruit with a fine flavor and although the fruit are small (2 to 5 g), mature vines can produce up to 12 kg of fruit (Gotsik 1955). These can contain more than 1% fresh weight vitamin C (e.g., Chesoniene et al. 2004). *A. kolomikta* has some commercial interest in more northerly regions as its great advantage is its cold-hardiness: it will survive and even flourish under conditions that most other *Actinidia*, even *A. arguta*, will not tolerate. Thus, it grows farther north than any other species, above 50°N, but it also extends to the south at higher altitudes and can occur at 3500 m in southwest China. It often proves difficult to grow under more temperate conditions. *A. kolomikta* occurs in two main, widely separated, discontinuous geographic regions (Li 1952; Deng and Ming 2003). Plants growing in western China (Shaanxi, Hubei, and Sichuan) tend to be more vigorous and to have broader leaves with browner, thicker hairs on the veins and more rigid hairs on the leaf surface, than the plants growing in northeast Asia. These differences were used to separate a west China variant as a distinct species (*A. gagnepaini* Nakai) or variety (*A. kolomikta* var. *gagnepaini* (Nakai) Li), but the differences are now considered (Liang 1984; Deng and Ming 2003) to be too slight and not constant enough to justify such separation.

Actinidia arguta is similarly one of the most widespread of all *Actinidia* species, being found in eastern Russia, Korea, and Japan and throughout much of China from Heilongjiang and Jilin in the north to high altitudes well south of the Yangzi River. Like many of the other *Actinidia* species that are widespread geographically, it is polymorphic, consisting of a number of variants that are morphologically distinct in leaf shape, flower characteristics, or vine hairiness. Some of these variants have been segregated into varieties, and one of the most distinctive is *A. arguta* var. *purpurea* which differs from the type variety in having relatively longer narrower leaves that are never setose, generally smaller flowers, and fruit that are long and dark purple. This variety has sometimes been treated as a distinct species, *A. purpurea* Rehder. The variants of *A. arguta* tend to have distinct geographic regions: *A. arguta* var. *purpurea* predominates in southwest China, whereas *A. arguta* var. *arguta* is mainly, although not exclusively, in northeast China, Japan, and Siberia (Li 1952; Cui 1993).

The main commercial advantages of *A. arguta* are its resistance to cold when fully dormant, the convenience of the fruit with their hairless, edible skins, and their appealing sweet, aromatic flavor (Williams et al. 2003).

B. Regional Distribution, Natural Habitats, and Wild Production

1. China. The Zhengzhou Fruit Research Institute, Chinese Academy of Agricultural Sciences (CAAS), coordinated a nationwide survey of *Actinidia* germplasm resources in China during 1978–1983, extended in some regions until 1990. The vast amount of information collected for the regions studied is described in Cui (1980, 1993), Cui and Huang (1982), and Cui et al. (2002).

There are relatively few undisturbed natural habitats in China and the clearance of forests for cultivation means that the distributions of many *Actinidia* taxa are now discontinuous and localized whereas once they were probably much more widespread. Vines are still being lost because of collection of firewood, collection for purposes such as making paper, or by being pulled down out of trees when fruit are harvested. Many taxa are considered endangered or locally extinct, including *A. chengkouensis*, *A. chrysantha*, *A. deliciosa* var. *chlorocarpa*, *A. grandiflora*, *A. guilinensis*, *A. henanensis*, *A. indochinensis*, *A. melanandra* var. *cretacea*, *A. pilosula*, *A. suberifolia*, *A. tetramera* var. *badongensis*, and *A. stellatopilosa* (Zhang 2000; Zhang et al. 2000). Inclusion of *A. chrysantha* and *A. indochinensis* in such a list of endangered taxa seems somewhat surprising as their fruit make up a significant part of the 5000 t of *Actinidia* fruit collected from the wild in Guangxi each year. Some of the varieties considered endangered are minor variants but most taxa are very distinctive, but limited in their distributions.

Actinidia species are now largely confined to more mountainous and remote areas. However, it does seem that the mountains are not just a place of refuge but may, indeed, be their preferred habitat; the abundance of *Actinidia* taxa is determined in large part by topographic complexity providing sites at a variety of altitudes and differing in microclimate at a particular latitude. The type of vegetation, the forest coverage and the soils are also important.

Biogeographic regions do not usually closely coincide with provincial boundaries. We therefore summarize the data on natural habitats and the regional distribution of *Actinidia* species in China from southwest to northeast according to the geographic regions:

southwest China	Yunnan, Guizhou, south and west Sichuan, Xizang (Tibet)
south China	Guangdong, Hainan, Guangxi, south Hunan
central China	Hubei, east Sichuan (Chongqing), west Hunan, south and southwest Henan, south Gansu, Anhui, south Shaanxi
east and southeast China	Jiangsu, Zhejiang, Jiangxi, Fujian, Taiwan
north China	Hebei, Shandong, Shanxi
northeast China	Liaoning, Jilin, Heilongjiang

Place names are transliterated as in the atlas *Zhonghua Renmin Gongheguo Fen Sheng Dituji* (1983).

Southwest China. Yunnan has more *Actinidia* taxa than any other province in China with a great diversity of species, varieties, and forms (Table 1.2), (Cui et al. 1990; Hu et al. 2003). This is in large part due to Yunnan’s complex topography: more than 90% of the total area of the province is in mountains and elevated, dissected plateaus, and only a small proportion is as dispersed valleys or isolated, relatively flat basins. To the west of Yunnan are the Hengduan Shan (Hengduan Mountains) and other mountain ranges that form a barrier rising to the Tibetan plateau. In the north, are parallel mountain ranges separating large rivers. Further south, the Yun-Gui (Yunnan-Guizhou) Plateau has overlapping mountain systems rising to some 4000 m above valley floors at about 1000 m. This very broken topography provides for many different habitats and for a great range of microclimates.

Yunnan has a humid monsoonal climate with distinct wet and dry seasons but, although spring is usually relatively dry, this does not normally inhibit growth of *Actinidia*. The many rivers and lakes maintain the relative humidity and provide moisture for the montane rains which are sufficient to satisfy plant needs. *Actinidia* usually grow on the sides of river valleys and are most abundant at altitudes between 700 and 2600 m. The forests of southern Yunnan are floristically rich and tropical because the annual rainfall is 1400 to 2000 mm and the relative humidity 70 to 85%. The average mean temperature throughout the province is about 15°C: in mid-winter (January), mean temperatures are between 8 and 17°C, in summer (July) between 11 and 29°C. In the warmer, southern areas, as around Hekou (Cui 1993), conditions are ideal for many of the subtropical species such as *A. henryi*, *A. indochinensis*, *A. latifolia*, and *A. suberifolia*. In such areas, nearly every day of the year has a mean temperature ≥ 10°C. However, at higher altitudes in the mountains of northwest Yunnan, temperatures can fall as low as –14°C in winter. Here the subtropical climate is tempered by the altitude.

The variable topography and the great range of microclimates explain why Yunnan has *Actinidia* species that are typical both of more northern China and southern China. Furthermore, many taxa are endemic to the province; some taxa are widely dispersed but many others are limited to only a single county or even part of a single county. For example, in northwestern Yunnan, close to the Hengduan Shan, some taxa occur exclusively on the western slopes of canyons of the high, steep mountains, while other taxa are restricted to the eastern slopes. Taxa may also occur within restricted altitudinal zones: some at higher altitudes, others at lower altitudes. Such strict zonation helps account for the rapid evolution that *Actinidia* appears to be undergoing. Unfortunately, when taxa are limited to such localized areas, they can readily be endangered through human activity. Northeastern and eastern Yunnan are the southwestern limit to the distribution of *A. chinensis* and *A. deliciosa*: the quantities of fruit of these species collected from the wild in Yunnan are therefore small.

The high mountains of northwestern Guizhou have a cold montane climate with heavy frosts in winter. Southern Guizhou forms part of the Yun-Gui Plateau with deep valleys, sometimes descending to 500 m, along the three main rivers, the Nanpan Jiang, the Hongshui He, and the Duliu Jiang. There the climate is that of the warm and moist, subtropical zone. As in Yunnan, the complex topography and the many different microclimates have resulted in great diversity in the abundant *Actinidia* taxa. Three quarters of these taxa are in southeastern and southern Guizhou or in the Tongren district (eastern Guizhou) at altitudes from 600 to 1400 m, and where the annual rainfall is 1100 to 1400 mm. Most taxa there are of localized distribution and occur only over narrow altitudinal ranges. In contrast, *A. callosa* var. *henryi*, *A. chinensis*, and *A. deliciosa* are widespread throughout much of the province and can occur over a wide altitudinal range. *A. chinensis* and *A. deliciosa* can tolerate drier conditions than can most of the other *Actinidia* taxa found in Guizhou and they will therefore grow in areas where the annual rainfall is as low as 970 mm: *A. deliciosa* is found almost everywhere throughout the province between 400 and 2300 m as long as climatic conditions are suitable; *A. chinensis* is also widespread but less abundant, between 700 and 1900 m. The annual natural production of *Actinidia* fruit is about 10,000 t, mostly of *A. deliciosa* (Table 1.5).

Sichuan is a large and diverse province in terms of topography and climate and this has consequential effects on the abundance and distribution of *Actinidia* taxa. The more eastern areas of the province are best considered as part of the central China region, separate from the western and southwestern areas discussed here. The western area that is richest in *Actinidia* can itself be divided into two main parts, the mountains bordering the Red Basin (of which the Chengdu Plain forms part), and, farther west, the foothills to the Tibetan plateau. The annual collection of *Actinidia* fruit from the wild (mainly *A. deliciosa*) in the western and southern regions of Sichuan is estimated to be about 10,000 t.

In the Red Basin itself, little remains of the original vegetation. There are few *Actinidia* species and the amount of fruit collected from the wild is insignificant: *A. deliciosa* would be the most common species, mainly at altitudes from 600 to 1000 m. The western boundary of the Red Basin is formed by a narrow band of mountains that stretch southwest from the Longmen Shan (Longmen Mountains), close to the Gansu border. The most notable of this band of mountains is Emei Shan (Mt Emei or Mt Omei), one of China’s four most sacred mountains and famous among early plant explorers for its extraordinarily rich flora. This region has a humid climate (relative humidity generally close to 85%), plentiful rainfall rising from 1300 mm to some 2000 mm, and a long frost-free period

Table 1.5. Chinese commercial kiwifruit plantings, commercial production, and collection of kiwifruit from the wild, 2004. Provinces are generally listed from southwest to northeast. Data were collated at the Annual Meeting of the *Actinidia* Section, Chinese Society for Horticultural Science, Shishou, Hunan, 18–20 October 2004.

Province	Plantings (ha)	Production (t)	Harvest from wild (t)
Yunnan	300	1,500	1,800
Guizhou	6,700	37,500	10,000
Sichuan	8,300	19,500	24,300
Xixang	—	—	—
Guangdong	2,000	7,000	1,250
Hainan	—	—	—
Guangxi	1,000	5,000	5,000
Hunan	5,300	35,000	22,900
Hubei	2,300	8,000	22,500
Henan	5,700	3,000	14,300
Anhui	2,000	20,000	8,000
Gansu	—	—	2,500
Shaanxi	16,000	200,000	22,000
Jiangsu	700	2,300	—
Zhejiang	6,700	26,000	5,000
Jiangxi	5,000	17,000	11,100
Fujian	2,500	20,600	3,500
Taiwan	—	—	—
Hebei	—	—	3,000
Shandong	—	—	—
Shanxi	—	—	—
Beijing	—	—	75
Liaoning	—	—	6,000
Jilin	—	—	3,000
Heilongjiang	—	—	—
Total	64,500	402,400	166,225

of 270 to 300 days depending on altitude. The vegetation changes with altitude from subtropical to warm temperate evergreen broadleaf forests to cool temperate forests with deciduous trees and shrubs or conifers dominant. *Actinidia* relish such conditions and they are abundant and widespread, particularly in Qinchuan, Beichuan, Pingwu, Guangyuan, Meigu, Emei Shan, Tanquan, and Ebian. They grow at altitudes from 700 to 2600 m, but are most abundant between 900 and 1600 m. The most common and widespread species is *A. deliciosa*, and other taxa that are particularly common include *A. callosa* var. *henryi*, *A. rubricaulis* var. *coriacea*, and *A. polygama*. Taxa with more limited distributions include *A. rubus*, *A. vitifolia*, *A. grandiflora*, *A. leptophylla*, other varieties of *A. callosa*, *A. venosa*, *A. venosa* f. *pubescens*, *A. arguta* var. *purpurea*, *A. melanandra*, *A. tetramera*, *A. kolomikta*, and *A. maloides*. Remarkably large, pure stands of *Actinidia* have very occasionally been found, e.g., a 1400 ha stand of *A. polygama* near the Jubei Peak of Mt Emei or a 700 ha stand of *A. maloides* (now included by some taxonomists in *A. kolomikta*) in Shuanshuijing. Such large, continuous patches of *Actinidia* are rarely seen in China.

Sichuan west of the mountains forming the western boundary of the Chengdu basin comprises a huge area rising in altitude to the Tibetan Plateau with its high mountains and deep gorges. There are big changes in climate, soils, and vegetation progressing west from lower to higher altitudes: mean annual temperatures fall from 10 to 15°C to below zero, and the frost-free period drops from 210 to 270 days so that, eventually, frost can occur any day of the year. The average annual rainfall is between 500 and 900 mm and the relative humidity is low at c. 60%. The natural vegetation ranges from xerophytic shrub forests in the valleys and foothills to montane coniferous forests to high alpine vegetation. This combination of conditions is quite unsuitable for almost all *Actinidia*: *A. deliciosa* is sometimes found below 2500 m, *A. arguta* var. *purpurea* and *A. callosa* var. *henryi* also occur in scattered locations, but *A. tetramera* is somewhat more widespread. The annual production of fruit from the wild in this region is about 1000 t.

The climate of most of Xizang (Tibet) is unsuitable for nearly all *Actinidia*. The few taxa that are present (*A. carnosifolia* var. *glaucescens*, *A. cinerascens* var. *longipetiolata*, *A. fulvicoma*, *A. leptophylla*, *A. liangguangensis*, and *A. venosa*) are restricted to valleys and the edges of rivers in the eastern Himalayas, along the Yarlung Zangbo Jiang (which eventually feeds into the Brahmaputra) and the southern parts of the Hengduan Shan along the border with Sichuan. Even in these regions, between 2050 and 3100 m, conditions are not ideal: the annual average temperature is only 5 to 12°C, the maximum can be over 30°C and the minimum between –4.5°C and –20°C. There are only 130 to 200 frost-free days and the annual rainfall is between 280 and 760 mm with the annual relative humidity less than 70%.

The southwestern part of Sichuan, south of Emei Shan, has mild winters and relatively cool summers with distinct wet and dry seasons. The mean annual temperature is 13 to 18°C, the annual rainfall is 900 to 1100 mm, the relative humidity is 70 to 80%, and the frost-free period 220 to 300 days. With increase in altitude, the vegetation changes from sparse grass and shrubs to Yunnan pine forests, evergreen, broadleaf forests, coniferous forests and, finally, to subalpine vegetation. *Actinidia* taxa are found almost everywhere within this region but are particularly abundant in Shimian and Hanyuan Counties, between the Daxiang Ling (the Daxiang Mountains) and the Xiaoxing Ling (the Xiaoxing Mountains), followed by Zhaojue, Ganluo, Mianning, and Jingyang counties. *Actinidia* usually grow between 1000 and 3500 m, and are especially common between 1200 and 1800 m. *A. deliciosa* is the most widespread species in the region, followed by *A. callosa* var. *henryi*, *A. venosa*, *A. arguta* var. *purpurea*, *A. kolomikta*, and *A. polygama*. Taxa with much more limited distributions include *A. melanandra*, *A. rubricaulis* var. *coriacea*, *A. leptophylla*, *A. rubus*, *A. tetramera*, *A. vitifolia*, *A. callosa*, *A. venosa* f. *pubescens*, and *A. maloides*. About 2000 t of fruit are collected from the wild each year.

South China. This region consists of the provinces of Guangdong, Hainan, Guangxi, and the southern part of Hunan. Guangdong has a warm subtropical climate with mild winters, plentiful rain, and high relative humidity. Much of northern Guangdong is mountainous and this provides different habitats and microclimates at various altitudes that suit individual *Actinidia* taxa. Thus, although *Actinidia* occur in many parts of the province, they are most abundant in the mountain ranges close to the border with southern Hunan and eastern Guangxi, where some individual counties may have 10 to 14 different *Actinidia* taxa. In such areas, the mean annual temperature is typically 19 to 20°C, the average temperature in January (winter) is 9 to 10°C, and in July (summer) is 28 to 29°C, and the annual rainfall is 1500 to 1800 mm.

Actinidia latifolia is the most widespread of all species, found throughout most of Guangdong and extending south into areas such as Hong Kong, where it is the only *Actinidia* to occur. Other species that are widespread include *A. carnosifolia*, *A. eriantha*, *A. fulvicoma*, *A. glaucophylla*, and *A. melliana*. Many taxa, however, have very limited distributions, e.g., *A. macrosperma* is restricted to Ruyuan County (close to the border with southern Hunan), *A. indochinensis* to Xinyi County (south-eastern Guangdong), and *A. cinerascens* var. *tenuifolia* to Jiaoling County (near the border with Fujian). *A. chinensis* is found only in Lechang, Ruyuan, and Yangshan, also close to the Hunan border.

The island of Hainan, to the south of Guangdong, is between latitudes 35° 8′N and 20° 10′N. It has a tropical monsoon climate with an annual average temperature of 22 to 26°C and an annual rainfall of 1500 to 2000 mm. More than 300 days each year are sunny. These climatic conditions are unsuitable for most *Actinidia* species: only two are present on the island, *A. latifolia*, common in much of southern China and farther south, and *A. melliana*, also found in western Guangdong (Chun et al. 1964).

The province of Guangxi is especially rich in *Actinidia* resources, both in terms of plant abundance and in diversity of taxa (Table 1.2). Although *Actinidia* are found throughout much of Guangxi, the greatest diversity and abundance is in the mountains where, as in other provinces, the broken topography provides for different habitats and varying microclimates suitable for individual taxa. The many river valleys also provide suitable environments for *Actinidia*. The annual rainfall in most areas in which *Actinidia* are found is between 1050 and 1950 mm, and the relative humidity 75 to 85%. The climate of northern Guangxi could be considered temperate to subtropical, that of the southern parts definitely subtropical.

Three areas in Guangxi are particularly rich in *Actinidia*. In northeastern Guangxi, towards the borders with Guizhou and Hunan, the Yuecheng Ling (Yuecheng Mountains), Haiyang Shan (Haiyang Mountains), and Dayao Shan (Dayao Mountains) all running from northeast to southwest and the Jiuwan Dashan ranges rise above 1500 m. Here there are many taxa. For example in Sanjiang, Ziyuan, and Rongshui counties, north of Guilin, more than 10 taxa are found in each county, including numerous plants of the commercially important taxa, *A. chinensis*, *A. deliciosa*, *A. deliciosa* var. *chlorocarpa*, and *A. chrysantha*. In northwest Guangxi, *Actinidia* are also abundant, mostly in the eastern Daming Shan (Daming Mountains) and Duyang Shan (Duyang Mountains), north of the Nei Jiang (Nei River), where the altitude ranges from 500 to 1000 m. The third main area of distribution is south and southeastern Guangxi where the hills and low mountain ranges rise to about 1000 m.

Actinidia latifolia is very common in Guangxi: it occurs mainly in areas in which the mean annual temperature is 16 to 22°C, the average in July is between 26 and 29°C with a maximum of 40.4°C, and in January the average is between 6 and 15°C, the extreme minimum measured being 2.3°C. *A. chinensis* grows in north and northeastern Guangxi, where the mean annual temperature is between 16 and 20°C, the average temperature is between 26 and 29°C in July, with a maximum of 40.4°C, and 6 to 9.5°C in January, the extreme minimum being –8.4°C. *A. chinensis* is generally not damaged by frost, but yields are sometimes affected by unseasonal cold fronts coming down from the north bringing snow and freezing temperatures to the mid and high mountain areas. *A. indochinensis* occurs in southern Guangxi, where the mean annual temperature is 19 to 22°C, the average temperature in July is 24 to 27°C with a maximum of 40.8°C, and in January the average temperature is 9 to 16°C with an extreme minimum of 0.2°C. *A. indochinensis* is adapted to higher temperatures than many other *Actinidia* taxa.

Each year about 5000 t of *Actinidia* fruit are collected from the wild in Guangxi (Table 1.5): *A. latifolia* about 2000 t; *A. chinensis*, *A. deliciosa*, and *A. deliciosa* var. *chlorocarpa* about 1500 t, and *A. eriantha*, *A. chrysantha*, *A. indochinensis*, *A. callosa* var. *henryi*, and *A. fulvicoma* var. *lanata* f. *hirsuta* about 1250 t.

Actinidia are also abundant in the areas of south Hunan adjacent to the borders with Guangxi and Guangdong, predominantly in the Nan Ling (Nan Mountains) in Jianghua, Jiangyong, and Yizhang Counties. The most abundant species are *A. chinensis* and *A. eriantha*, but *A. callosa* var. *henryi*, *A. chrysantha*, *A. glaucophylla*, *A. latifolia*, *A. liangguangensis*, and *A. melliana* are also common. Annual production from the wild in this part of Hunan is about 3450 t.

Central China. This region includes Hubei, eastern Sichuan (Chongqing), western Hunan, southern and southwestern Henan, Anhui, southern Gansu, and southern Shaanxi.

Topographically, Hubei consists of a low, flat, U-shaped central basin opening toward the south and surrounded by mountains to the west, north, and east. Generally, altitudes are lower in the east and higher in the west and the mountains in the southwest form a continuation of the Yun-Gui Plateau. Parts of the province are almost at sea level, whereas Mt Dashennonjiang to the west, the highest peak in central China, reaches 3053 m. More than half the area of Hubei is in mountains and another quarter is in high hills. Hence, there are large differences in altitude providing a wide range of ecological habitats. Two major rivers, the Yangzi and the Han Shui run through the province as well as almost another 1200 medium and small rivers. There are at least a thousand lakes of varying size (the reason for Hubei being sometimes being called the "province of lakes").

Hubei has a subtropical monsoonal climate zone with distinct seasonal changes. In most parts of the province, the mean annual temperature is between 15 and 17°C, the average temperature in July is 27 to 29°C, nearly 30°C in the southeast, the frost-free period is 230 to 300 days. The annual rainfall is 750 to 1600 mm but can be up to 1800 to 2000 mm in alpine regions. Summer rains can account for 35 to 50% of the total annual precipitation, and rainfall usually decreases in early autumn. There are 1800 to 2000 hr sunshine.

Actinidia in Hubei occur predominantly throughout the western and southwestern mountain ranges, mainly the Wudang Shan, Daba Shan, Wuling Shan, and Dalou Shan mountains, and the high hills west of Yichang. Individual taxa occur at very different altitudes: they are generally found anywhere between 100 and 2000 m although *A. kolomikta* occurs as high as 2800 m on Mt Dashennonjiang. *A. chinensis* may be found as low as 100 m and other taxa that often occur below 500 m include *A. deliciosa*, *A. eriantha*, *A. latifolia*, *A. rubricaulis* var. *rubricaulis*, and *A. rubricaulis* var. *coriacea*. Between 800 and 1200 m *A. chinensis* and *A. deliciosa* are particularly common. Taxa that normally occur above altitude 1000 m are all those that have been placed in the *Leiocarpae*, the most cold-hardy section of the genus: *A. arguta* var. *arguta*, *A. arguta* var. *purpurea*, *A. arguta* var. *giraldii*, *A. arguta* var. *cordifolia*, *A. kolomikta*, *A. macrosperma*, *A. maloides*, *A. tetramera* var. *tetramera*, and *A. tetramera* var. *badongensis*. The annual production of *Actinidia* fruit from the wild in Hubei, mainly fruit of *A. chinensis* and *A. deliciosa*, is estimated to be approximately 22,500 t (Table 1.5).

Eastern Sichuan (Chongqing) can be divided into two parts. North of the Yangzi, the eastern boundary of the great Red Basin of Sichuan is formed by the southern slopes of the Micang Shan and Daba Shan, the western slopes of the Wu Shan (mountains mainly in Hubei), and a series of lower mountain ranges such as the Guanmian Shan. South of the Yangzi, there are lower mountains such as the Fangdou Shan rising toward the borders with Hubei and Guizhou.

In the part of eastern Sichuan north of the Yangzi, the climate is colder and wetter than that of the mid-subtropics: the mean annual temperature is 14 to 16°C and the frost-free period is 250 to 270 days. The annual rainfall is 1100 to 1400 mm, decreasing gradually from east to west, and the relative humidity is 75%. Depending on the altitude, the natural vegetation is subtropical, evergreen broad-leaved forests at lower altitudes, above which are mixed mountain evergreen and deciduous broad-leaved forests or mountain coniferous forests at higher altitudes. *Actinidia* species are found almost everywhere throughout the region. The most common species is *A. deliciosa*, followed by *A. rubricaulis* var.

coriacea, *A. callosa* var. *henryi*, *A. polygama*, *A. trichogyna*, *A. arguta* var. *purpurea*, *A. melanandra*, *A. kolomikta*, and *A. tetramera*. There are also some taxa endemic to the region: *A. chengkouensis*, *A. stellatopilosa*, and *A. arguta* var. *nervosa*. A distinctive feature of *Actinidia* distribution in this region is the numerous areas, often more than 100 ha, consisting of many plants of an individual taxon growing close together. More than 5000 t of fruit are collected annually from the wild.

South of the Yangzi, the climate is somewhat milder and wetter, more typical of the subtropics. The annual average temperature across this region is 10 to 16°C with 265 to 310 frost-free days. The annual rainfall is 1200 to 1500 mm, although not evenly distributed throughout the year. The most widespread natural vegetation is subtropical, evergreen broad-leaved forests with some coniferous or bamboo forests. *Actinidia* taxa are abundant, especially between 600 and 1500 m. The most common taxa are *A. deliciosa*, *A. callosa* var. *henryi*, and *A. rubricaulis* var. *coriacea*. Collection of fruit from the wild is again important: more than 5000 t per year.

Hunan declines in altitude from west to east with the central plains, opening to the north where there are many lakes, bordered by mountains to the east, south, and west. There are only scattered *Actinidia* in the central and northern parts of the province and *A. chinensis* is the most common species. In eastern Hunan, east of Changsha, *Actinidia* are found in the hills and mountains that stretch from the Mufu Shan in the north to the Wugong Shan in the south. This is a relatively warm area with typically less hardy species such as *A. chinensis*, *A. eriantha*, and *A. latifolia*. South Hunan is considered separately as part of the south China region.

West Hunan lies within the center of diversity of the genus. *Actinidia* are abundant throughout the length of the Wuling Shan (Wuling Mountains), south from Cili, Shimen and Sangzhi Counties, close to the border with Hubei, to Yongshun and Longshan Counties, near the Sichuan border, south again to Jishou, Fenghuang, and Mayang, close to the border with Guizhou, and then farther south again to the Xuefeng Shan (Xuefeng Mountains) east of Huahai, mountains that merge with those forming a northern extension of the Yun-Gui Plateau. There, in Jingzhou and Chengbu Counties, the most southwestern part of Hunan, *Actinidia* are also abundant.

Actinidia chinensis and *A. deliciosa* are the predominant *Actinidia* taxa and are usually accompanied by *A. callosa* var. *henryi*, *A. latifolia*, *A. arguta* var. *pupurea*, *A. rubricaulis* var. *rubricaulis*, and *A. rubricaulis* var. *coriacea*. West Hunan accounts for about 60% of the total annual production from the wild in Hunan province, about 23,000 t (Table 1.5).

Henan has mountains to the north, the west, and the south. The major river, the Huang He (Yellow River), one of the most important in China, flows across the north of the province. *A. arguta* and *A. polygama* occur sporadically in the Tainhang Shan mountains which extend into northern Henan, north of the Huang He, but *Actinidia* are much more abundant in southwestern and southern Henan. The Funiu Shan are high mountains to the west of the province and here *A. chinensis* and *A. deliciosa* are the most important species. In the Tongbai Shan and the Dabei Shan, lower mountains along the border with Hubei, *A. chinensis* is abundant. *A. chinensis* and *A. deliciosa* grow mostly at altitudes 350 to 1200 m, and are seldom found below that. Very few *Actinidia* taxa occur below altitude 100 m, and the numbers also decrease above 1200 m. In the areas in which *A. chinensis* and *A. deliciosa* are common, the mean annual temperature is between 11.3 and 15.8°C, the maximum temperatures between 35 and 43°C and the winter minimums from –6.0 to –18.7°C with a frost-free period ranging from 180 to 250 days. Annual rainfall varies considerably from 600 to 900 mm in the Funiu Shan rising to 1050 to 1350 mm in the Tongbai Shan.

A total of 12 *Actinidia* taxa are found within Henan, including *A. arguta* var. *arguta*, *A. arguta* var. *purpurea*, *A. callosa* var. *henryi*, *A. chinensis*, *A. deliciosa*, *A. henanensis*, *A. kolomikta*, *A. melanandra*, *A. rubricaulis* var. *coriacea*, *A. tetramera*, and *A. valvata*. The annual production from the wild is about 14,000 t, of which about 65% is likely to be of *A. deliciosa*.

In Anhui, *Actinidia* are found mainly in the Dabie Shan, mountains in the southwest of the province that continue into Hubei, and in the mountainous regions, the Huang Shan, southeast of the Yangzi. In these areas the climate is typically temperate, the mean annual temperature is 14.5 to 16.6°C, there are 210 to 255 frost-free days and the annual rainfall is up to 1680 mm. The most important species in Anhui is *A. chinensis* and about 8000 t of fruit are collected annually from the wild.

Actinidia in Gansu are largely restricted to the mountainous regions in the southeast, an extension of the Qin Ling mountains of Shaanxi. The topography is complex with overlapping mountain chains and valleys. This is the northernmost boundary of the subtropical or warm temperate, moist climatic zones and farther to the north, conditions are less favorable for most *Actinidia* species. *A. deliciosa* grows in areas where the annual mean temperature is above 10°C, the annual rainfall is 450 to 850 mm (but barely adequate), the relative humidity is above 60%, and there are more than 210 frost-free days per year. *A. deliciosa* in Gansu occurs between 660 and 1600 m, but is most abundant at altitudes 800 to 1300 m. *A. tetramera* is noteworthy for being more hardy and can grow in areas in which the annual mean temperature is above 5°C and the rainfall is above 400 mm per year. It can be found at 600 to 2700 m. About 2500 t of *Actinidia* fruit are collected from the wild each year, mostly fruit of *A. deliciosa*.

In Shaanxi *Actinidia* are limited to the south of the province, from about Xi'an southwards. They are found in the Qin-Ba Mountain ranges, which are divided by the Han River into the Qin Ling Mountains to the north and the Ba Shan Mountains to the south. The Qin Ling escarpment has steep northern slopes ascending to about 1500 to 3000 m but more gentle southern slopes gradually decreasing in height, with a rich diversity of forests. The topography and microclimates on these southern slopes provide favorable habitats for *Actinidia*. The Ba Shan consist of several ranges of mountains, at an altitude of 1500 to 2000 m running from northwest to southeast between northeast Sichuan and south Shaanxi.

The Qin-Ba mountains can be divided into two climate zones through the combined effects of geography, the monsoon, and topography: those parts of the southern slopes of the Qin Ling at around altitude 1000 m, which in general have a cool temperate climate, and the remainder of the area with more subtropical conditions during summer. There are distinct wet and dry seasons and frequent fluctuations in temperature, with a warm, dry spring followed by a hot, moist summer, a rather humid autumn, and a cold dry winter. The annual rainfall is 650 to 1214 mm.

Eight *Actinidia* taxa are found in the Qin-Ba Mountains: *A. deliciosa*, *A. polygama*, *A. tetramera*, *A. kolomikta*, *A. arguta*, *A. melanandra*, *A. callosa* var. *henryi*, and *A. chengkouensis*. *A. deliciosa* is the most common and the most widely distributed. About 22,000 t of fruit are collected from the wild each year.

East and Southeast China. This region comprises the provinces of Jiangsu, Zhejiang, Jiangxi, and Fujian, and the island of Taiwan. Although Taiwan is close to the mainland, its flora is very distinctive and about one quarter of its higher plants are endemic.

Jiangsu consists mainly of low-lying plains, less than 50 m above sea level, and no more than 5% of the total area is in hills. To the north, the only hills are in Xuzhou and Lianyungang, with the highest mountain there, Mt Yuntai, reaching 625 m. The hilly areas in the south on the western side of the Yangzi River delta and along the borders with Anhui and with Zhejiang do not exceed about 500 m in altitude. The forests in the north with a predominance of deciduous broadleaf trees differ from those in the south, which are evergreen and have subtropical components. Jiangsu stretches over the transition from the warm temperate climate zone in the north to a subtropical, humid, monsoonal climate in the south. The mean annual temperature is 13 to 16 °C, there is a long frost-free period of about 200 to 240 days, and the annual rainfall is 800 to 1200 mm, half of which is in summer. Although these climatic conditions should be very suitable, the wild *Actinidia* resources of Jiangsu are actually surprisingly limited. Only four taxa are now found: *A. chinensis* var. *chinensis*, *A. valvata* var. *valvata*, and *A. macrosperma* var. *mumoides* occur occasionally on the edges of forests and scrub in the hills of Yixing city and in Jiangning County, in the south of Jiangsu, and *A. arguta* var. *arguta* is sporadically found in the hills of Lianyungang city in the northeast. *A. kolomikta*, *A. polygama*, and *A. macrosperma* var. *macrosperma* have been recorded from Jiangsu but seem to be no longer present.

In contrast, nearly three quarters of Zhejiang, particularly the southwest part of the province, is in hills or mountains and the only relatively flat part of the province is toward the coast in the northeast. The many mountain ranges with their steep-sided valleys combined with the subtropical monsoonal climate create warm moist conditions ideal for *Actinidia*. In general, the mean annual temperature is 16°C, the maximum 42°C and the extreme minimum –21°C with 260 to 300 frost-free days. The average annual rainfall for the province is 1500 mm, but this increases to 1700 to 2000 mm in the more mountainous areas of west and southwest Zhejiang. There are 11 species and 5 varieties of *Actinidia* in Zhejiang, mainly in the Tianmu Shan (Tianmu Ranges) north of Hangzhou and along the border with Anhui, the Xianxia Ling, along the border with Jiangxi, and the Donggong, Yandang and Kuocang Shan, the mountains in the southwest adjoining Fujian. In this last area, *Actinidia* usually occur at altitudes 300 to 1600 m, mainly at 600 to 1000 m. *A. chinensis* is the most common species with about 5000 t being collected annually from the wild, followed by *A. eriantha*, varieties of *A. callosa*, varieties of *A. arguta*, and *A. melanandra*.

Much of Jiangxi is also in hills or mountains surrounding the central lowlands opening northeast to the Yangzi. The province has a warm, humid, subtropical climate. The mean annual temperature is 17 to 20°C, the mean January temperature 3.6 to 8.5°C and the mean July temperature 26 to 30°C, increasing from north to south. In the north, in the areas where *Actinidia* mostly grow there are some 240 frost-free days rising to about 310 days in the south. The annual rainfall is 1350 to 1930 mm, half of which falls between April and June and another quarter between July and September. Typically, therefore, Jiangxi has a wet spring and a hot, relatively dry summer. Jiangxi is rich in *Actinidia* taxa: 27 different taxa are recorded throughout the province, but they are particularly common in the mountains of the northwest, the Jiuling Shan and Mufu Shan, the mountains in the west adjoining Hunan, the Wuyi Shan mountains bordering Fujian, and the Haiyu Shan in eastern Jiangxi toward Zhejiang. *A. chinensis* is very widespread followed by varieties of *A. callosa*, *A. eriantha*, *A. lanceolata*, and *A. latifolia*. About 11,000 t of fruit, mainly of *A. chinensis*, are collected from the wild annually.

The coastal plains of Fujian comprise only about 10% of the total area of the province and the remainder is as hills or mountains: three quarters of Fujian consists of low (500 to 800 m) or medium height mountains (above 800 m). The complex topography and the various microclimates provide suitable habitats for *Actinidia* across the 5 main mountain ranges, the Wuyi Shan bordering Jiangxi, the Tailao Shan, and the Daiyun Shan, Jiufeng Shan, and the Boping Ling, extending parallel to the coast from southwest to northeast. *Actinidia* taxa are particularly common and frequent at altitudes above 800 m. Fujian has a warm humid subtropical climate subject to the monsoon. There are distinct differences in climate between the north and the south and between inland and coastal areas or between different altitudes. The mean annual temperature throughout the northern part of the province in which *A. chinensis* is widespread is 16.9 to 19°C, with maximum temperatures reaching 40°C in January and the minimum winter temperatures, –9.6°C. In these regions there are 230 to 317 frost-free days. The annual rainfall throughout the province is 1100 to 2100 mm increasing from northwest to southeast. There are very distinct wet and dry seasons with 50 to 60% of the annual rainfall from March to June and another 20% from July to September followed by a dry period from October to February. In regions where *A. chinensis* is common, the annual rainfall ranges between 1540 and 2100 mm. Eighteen *Actinidia* taxa are found in Fujian of which *A. chinensis*, mainly in the north, and *A. eriantha*, throughout the whole province, are the most common, followed by varieties of *A. callosa*, *A. hemsleyana*, *A. lanceolata*, and *A. latifolia*. About 3500 t of *Actinidia* fruit are collected from the wild each year of which *A. chinensis* accounts for 2000 t and *A. eriantha* 1500 t.

Taiwan has a particularly rich flora because it contains elements of both the holoarctic and palaeotropic floras. Two-thirds of the total area of Taiwan consists of forested mountains and the remaining area of hills, plateaus and highlands, coastal plains, and basins. The Central Mountain Range stretches along the entire island from north to south, thus forming a natural line of demarcation for rivers on the eastern and western sides of the island. On the west side lies the Yushan Mountain Range with its main peak reaching 3952 m, the highest mountain in

Taiwan. This varied topography allows for a variety of ecological niches and the mountains provide isolated habitat "islands." The flora of the lowlands in the south of the island is typically subtropical, the plants growing at middle altitudes resemble those of Japan and northern China, and at the higher altitudes, plants are similar to those of the Himalayas and western China.

The climate of Taiwan belongs to the oceanic monsoon pattern of the subtropics and tropics. The weather is warm throughout the year, with an annual average temperature of 22°C, 13 to 20°C in January, and 24 to 29°C in July. There are big fluctuations in weather conditions during winter and spring, but during summer and autumn the weather is relatively stable. The annual rainfall is about 2000 mm, and as high as 5000 mm in some areas in the mountains.

Eight *Actinidia* taxa are found on Taiwan, one of which, *A. setosa*, appears to be endemic (Li 1952, 1976; Nee and Tsay 1992; Peng and Lu 2003)—other taxa previously considered as endemic have been submerged into taxa found on the mainland. *A. arguta* is found in the central mountains above 1800 m as is *A. callosa* var. *ephippioidea* whereas *A. callosa* var. *callosa* occur in thickets and forests at low to medium altitudes. *A. setosa* (closely related to *A. chinensis* and *A. deliciosa*) is at altitudes between 1300 and 2600 m. *A. rufa*, otherwise found in Japan and Korea, is at high altitudes in the northern part of the island. *A. tetramera* is also present at higher altitudes, whereas *A. rubricaulis* occurs at lower altitudes. *A. latifolia*, also found in southwest China, Cambodia, Indonesia, Malaysia, Vietnam, and Cambodia, is widespread at altitudes between 500 and 1500 m.

North China. Climatic conditions in Hebei, Shandong, and Shanxi are severe, particularly during winter, and only a few cold-hardy *Actinidia* species are found in this region.

The three *Actinidia* species found in Hebei (including Beijing) all belong to the *Leiocarpae*: *A. arguta*, *A. polygama*, and *A. kolomikta*. They occur mainly in the Yan Shan (Yan Mountains), northeast of Beijing, and the Taihang Shan (Taihang Mountains) to the west of the province along the border with Shanxi. In areas where these species are most common, the mean annual temperature is 7 to 10°C, the maximum 38 to 40°C, the minimum –21 to –30°C, and there is a relatively short frost-free period of 170 to 190 days. *Actinidia arguta* is the most widespread species and is common in the mountains. In the Yan Shan (Yan Mountains) it can be found over a wide altitudinal range between 150 and 1500 m. About 3000 t of *A. arguta* fruit are collected from the wild each year (Table 1.5). *A. kolomikta* and *A. polygama* occur more sporadically, usually between 800 and 1000 m, in sunny and semi-shady areas of forest margins and gullies in the Heinongdong Shan, Heping Shan, and Huling Shan (mountains).

Only two species, *A. arguta* and *A. polygama*, occur in Shandong. These are found mainly in the Tai Shan (Tai mountains) in central Shandong and in the Qi Shan, Lao Shan, and Kunyu Shan (mountains) of the Shandong peninsula. Climatic information from the Tai Shan, at an altitude (1530 m) at which the two species occur, indicates a mean annual temperature of only 5°C, a maximum temperature of 27°C, and a minimum temperature of –25°C. The frost-free period is only 135 days, and the relative humidity is low at 63% despite the relatively high annual rainfall of 1130 mm. There are just under 3000 hr sunshine.

Actinidia are found only to the very south of Shanxi between the Huang He and the Zhongtiaoshan mountains mainly between 700 and 2000 m. Six species are present of which *A. arguta*, *A. arguta* var. *purpurea*, *A. kolomikta*, and *A. melanandra* are the most common (Chang et al. 1995). The climate is relatively cold and dry, with most of the limited rainfall between July and September.

Northeast China. The three provinces of northeast China, Liaoning, Jilin, and Heilongjiang, are noted for their even more severe climatic conditions tolerated by only three *Actinidia* species, *A. arguta*, *A. kolomikta*, and *A. polygama*, species that are also found in neighboring Siberia and in northern Japan as well as at higher altitudes farther south in China. Winters are very cold but the maximum temperatures in summer can be surprisingly high.

In Liaoning, *Actinidia* are generally found only in forested regions and are largely restricted to an area about 350 km north-south by 250 km east-west centered on Mt Changbai Shan (eastern Liaoning). In this area the mean annual temperature is 6 to 8°C, the minimum temperature –31 to –37°C, with only 163 to 179 frost-free days, whereas maximum temperatures can reach 37°C. *A. arguta* is the most widespread, *A. polygama* is rare, and *A. kolomikta* is also less common, found at higher altitudes than *A. arguta* (Hao 1982). An estimated 6000 t of fruit are collected annually from the wild (Table 1.5).

In Jilin, the three same species, *Actinidia arguta*, *A. polygama*, and *A. kolomikta*, are found mainly in the Changbai Shan, Nangang Shan, Laoyie Ling, Mudan Ling, and Nonggang Shan, mountain ranges, which extend south into Liaoning Province, as well as in the low mountainous regions of central Jilin. In such areas, the mean annual temperature is 2.5 to 6.5°C, the maximum temperature 32 to 37°C and the minimum –34 to –45°C, with a frost-free period of 130 to 150 days. About 3000 t of *A. arguta* fruit are collected from the wild each year.

Heilongjiang, bordering Siberia, is the most northeastern province of China. The same three *Actinidia* species are again found, mainly in the Laoyie Ling and Wanda Shan (Laoyie and Wanda ranges), and on the southern slopes of the Xinan Ling (Xinan Range). The climatic conditions that occur where these three species are found can be particularly severe: the mean annual temperature is only 0.3 to 2.8°C, the minimum –39 to –43°C, but maximum temperatures can reach 34°C. *A. arguta* is the most cold-hardy species, surviving in the Yichun district even when temperatures fall below –43°C.

2. Amur Oblast, Khabarovsk Krai, and Primorski Krai, Russian Far East. Three *Actinidia* species are found in the Far Eastern Region of the Russian Federation. They are particularly abundant in the catchment areas of some of the larger rivers such as the Uda and the Amur, from about 128°E, and the Ussuri, in the Sikhote-alin Ranges.

Actinidia kolomikta is the most cold-hardy and extends north to 52°40'N, the northernmost of any *Actinidia* species. This far north, the climate is very harsh with average yearly temperatures well below zero. The rivers freeze over by November, and the winter minimum temperatures can fall to below –40°C. At the northern limit of its range or in more open, stony environments, *A. kolomikta* can be reduced to thickets several metres high consisting of procumbent and rooting vines (Berestova 1970). *A. kolomikta* does not do well in very dense conifer-broadleaf forests farther south but is more often found in worked-over forests that have been thinned or at the edges of forests and in clearings. It can grow into a vigorous climber, ascending more than 15 m up into trees and with a stem 4 to 6 cm in diameter. It was formerly very abundant so that, for example, in the middle Amur, forests were almost impassable (Stapf 1926), but the number of vines has been drastically reduced through the wanton cutting down of vines to collect fruit (FAO 1996). It grows best at altitudes between 500 and 900 m, but its altitudinal range varies with latitude: in the far north the upper limit is 150 to 500 m, in the south in the Primorski Krai, it can grow almost to 1800 m (Poyarkova 1949).

Actinidia arguta is restricted to the southern part of the Primorsky Krai, where it is found sporadically, often in small groups twisting around trees in conifer or conifer-broadleaf forests (Poyarkova 1949). In forests it can grow to 25 m (Vorobiev 1939), usually at altitudes between 150 and 800 m, depending on the rainfall and temperatures, but in coastal areas it can be reduced to scrambling among rocks or near springs.

Actinidia polygama, much rarer than *A. arguta* or *A. kolomikta*, is a less vigorous grower, and is limited to the Primorski Krai, where its most northern limit is about 2° south of that of *A. arguta* (Berestova 1970). It occurs at altitudes between 100 and 300 m. In some areas, all three *Actinidia* species can be found intertwining each other (Vorobiev 1939).

3. Sakhalin and the Kuril Islands. Sakhalin lies to the east of mainland Khabarovsk Krai and about 40 km north of Hokkaido, Japan. The climate is milder than that of the mainland but still relatively cool to cold and winter temperatures can descend to –30°C. *Actinidia* species are limited to the southern parts of the island: *A. kolomikta* extends north to about latitude 50°30'N (Kolbasina 1963, 1969). It grows mainly in coniferous forests to an upper limit of 450 to 500 m in the north and 650 m in the south. *A. polygama* and *A. arguta* have much more limited distributions and occur only in the south (Vorobiev 1939; Poyarkova 1949; Kolbasina 1963, 1970; Horikawa 1972).

Three taxa are also found on the most southerly of the Kuril islands (Horikawa 1972), although *A. polygama* is reported as being very rare and, locally, close to extinction (FAO 1996). *A. arguta* occurs on Kunashir, close to Japan, which has a relatively mild climate, with an average temperature in winter (February) of –4.7°C and an average in summer (August) of 16.6°C. The island is often covered by fog, especially in June and July and has largely broadleaf and coniferous forests. *A. kolomikta* is also on Kunashir and the next most northern island, Iturup (Horikawa 1972).

4. Japan. The four main islands of the Japanese archipelago stretch from about latitude 31°N to 45°N, latitudes that correspond to much of central and northern China. Japan’s geological history and complex topography allow for a rich flora with about one third of higher plants being endemic. The climate is more temperate than that of continental China and should allow the growth of many different *Actinidia* species. Indeed, climatic studies indicate that Shikohu, Kyushu, and southwestern Honshu are all suitable for commercial cultivation of *A. deliciosa* cultivars (Kamota et al. 1989). However, only 5 *Actinidia* species occur naturally in Japan (Ohwi 1965; Horikawa 1972, 1976) and 3 of these are the cold-hardy species common in northern China and Siberia. Thus *A. arguta* is found almost everywhere in mountainous regions throughout Japan: in southern and central Japan it occurs between sea level to an altitude of 1600 m, sometimes even to 1900 m, but in northern Honshu and Hokkaido it is seldom found above 600 to 700 m. *A.*

arguta is not in the Ryukus to the south of Japan. The closely related, endemic species, *A. hypoleuca* is found in Shikohu, Kyushu, and Honshu. *A. polygama* is also common in woods and thickets in the mountainous areas of Kyushu, Shikohu, Honshu, and Hokkaido and similarly the upper altitudinal limit decreases farther north. In southern Japan, *A. polygama* is common from the lowlands to about 2000 m, but in northern Honshu seldom occurs above 900 m, and in Hokkaido the upper limit is generally between 500 to 600 m. *A. polygama* is also not in the Ryukus.

The distribution of *A. kolomikta* is more limited: it occurs in northern Honshu, north of about latitude 35°N, and in Hokkaido. In central Honshu it is generally found at altitudes from 1000 to 2000 m, with occasional vines as low as 700 m or up to 2500 m. In Hokkaido, it is found from sea level to about 1000 m, and the upper altitudinal limit declines the farther north.

The northern limit of *A. rufa* is about 35°N, the southern limit for *A. kolomikta*, and it is common from 34°N south to about 24°N. It is largely restricted to the southeastern coasts of Shikohu and Honshu, the western half of Kyushu and the Ryukus south to Okinawa (Walker 1976). With a few exceptions, *A. rufa* is found between sea level and an altitude of 500 m.

5. Korea. The main peninsula of Korea is between latitudes 34° and 42°N, approximately the latitudes of Shanxi, Hebei, and Shandong of mainland China, and much of the flora is very similar to that of northern China. Although the climate of Korea allows the commercial cultivation of introduced *A. deliciosa*, mainly in the south, the only species distributed widely throughout mountainous regions of the country are *A. arguta*, *A. kolomikta*, and *A. polygama* (Li 1952; Shim and Ha 1999). The island of Che Ju (Jejudo), south of mainland Korea, is warmer and has a warm-temperate vegetation, with many of the plants similar to or identical to those growing in southern Japan. One such plant is *A. rufa*, not found in mainland China, but otherwise restricted to Taiwan and Japan.

6. Cambodia. *Actinidia latifolia,* present throughout southern China and south to Sumatra and Borneo, has been recorded (as *A. championi*) (Finet and Gagnepain 1907).

7. Laos. *Actinidia* latifolia has been collected (Li 1952).

8. Vietnam. Three species have been recorded (Merrill 1938; Li 1943, 1952; Ho and Duong 1960), although two of these might have been confused with *A. callosa*, which is possibly also present: *A. indochinensis*, also found in Guangxi and Yunnan, *A. petelotii*, possibly endemic, and *A. latifolia*.

9. Myanmar (Burma). *Actinidia callosa*, one of the most widely distributed of all *Actinidia* species, has been reported from eastern Myanmar (Nath 1960) and *A. pilosula* (sometimes treated as a variety of *A. callosa* and also found in Yunnan) from northern Myanmar (Li 1952).

10. Thailand. Two *Actinidia* species have been recorded (Li 1952; Keng 1972). *A. rubricaulis* is found in evergreen forests from 1600 to 1850 m in the northeastern provinces adjoining the border with Myanmar. This species is common in Yunnan and much of southwestern China. *A. latifolia* occurs in evergreen forests about 900 m, in the peninsular region at 7 to 8°N.

11. Malaysia and Indonesia. *Actinidia latifolia* is occasionally found on the Malay Peninsula (Perak, about 4°N), Sumatra, and Borneo (e.g., Mt Kinabalu, Sabah), and a very distinct form of *A. callosa* in Malaya, Sumatra, and possibly Java (4°S). Somewhat surprisingly, *Actinidia* appears not to have been reported from the Philippines.

12. Northern India. Two *Actinidia* species extend into northern India, Nepal, and Bhutan. *A. strigosa* appears to be very localized, being found only in Nepal and Sikkim at high altitudes, 2500 to 3000 m. *A. callosa* var. *callosa* is found in the Himalayas from Garwahl to Sikkim from about 1500 to 2200 m (Hara 1966; Li 1952).

IV. DOMESTICATION AND COMMERCIALIZATION OF KIWIFRUIT

A. Early Use in China, Japan, and Korea

Although *Actinidia* germplasm resources are widespread and abundant throughout much of China, systematic domestication and widespread cultivation of the genus in China have occurred only over the past 20 to 30 years. Nevertheless, occasional accounts in ancient Chinese literature indicate that sporadic attempts were made in the past to cultivate kiwifruit species, starting about 1200 years ago (Bretschneider 1893; Wong 1969, 1970; Sun et al. 1981; Yan 1981; Ferguson 1990c; Cui et al. 2002).

There may be even earlier descriptions of *Actinidia* in classic Chinese texts. Some authors (e.g., Xin 1983) have identified as *mihoutao* (the current Chinese name for the genus *Actinidia*) the *changchu* described in the *Shijing* [the Book of Odes or the Book of Songs], written between 1000 and 500 BCE. The *changchu* is described in the *Shijing*, *Maoshi* Vol. 7: 濕有萇楚, . . . "*the changchu grows in damp places, its branches and tendrils are slender, swaying with the wind, and its flowers and fruits are graceful and beautiful*." In the *Er Ya* [Beauty] (200 BCE, West Han Dynasty), chapter 13 records the *changchu* and gives an alternative name *yaoyi*. Five hundred years later Guo Pu (276–324 CE, Jin Dynasty) edited the *Er Ya* and concluded that the *changchu* or *yaoyi* was what was then named the *yangtao* (a common name widely used in local Chinese dialect for *Actinidia*) or *guitao*, described as having ". . . *leaves shaped like peaches, white flowers, seeds like tiny wheat grains and fruits resembling peaches*." However, the name *yangtao* has been used for several different plants and Yan (1981) concluded that the *changchu* and *mihoutao* were quite different plants that had been confounded and described as one because they had the alternative name of *yangtao* in common.

A more convincing account of what is probably *Actinidia* is given in the *Shanhaijing-Zhongshanjing* (the volume dealing with mountains in a geography encyclopedia of the *Zhanguo*, Warring States, 475–221 BCE): "*About 15 km east, there is mountain called Fengshan [Feng mountain] where there are many fengshi [a type of stone], plentiful mulberry trees and yangtao. The yangtao fruit are similar to a peach while the branches are more-or-less square in cross section. An alternative name is guitao [ugly peach]. The bark can be used for leather or paper. It can be used to cure inflammations*." The Fengshan is 15 km northeast from Nanyang, Henan and in that province, *Actinidia* are still given the common name of *yangtao*.

The first known use of the name *mihoutao* for *Actinidia* occurs in a poem by Cen Sen (714–770 CE) of the Tang Dynasty (618–907 CE). He describes an autumnal scene, mentioning an arbor or trellis of *mihoutao* above a well in the garden. The place names in the poem indicate a site in today's Shaanxi (Sun et al. 1981). This is the first record of an *Actinidia* plant being cultivated. The location suggests that it was possibly a plant of *A. deliciosa* that was being grown about 1200 years ago.

Cultivation can never have been widespread, as subsequent accounts in the great pharmacopoeias (*Bencao*) or encyclopedias describing the appearance and use of *mihoutao* as medicine, food or for industry consistently state or imply that they were wild plants. For example, the *Chongxiu Zhenghe Jingshizhenglei Beiyong Bencao* [Flora for the Revision of Political and Historical Texts] (first written during the Northern Song Dynasty in 1108, and revised subsequently in 1249 by Tang Shen-wei) states that *mihoutao* grew in the mountain valleys and were vines that climbed over trees. The leaves were round and hairy, the fruit were similar in size and shape to eggs, and they had brown hairy skins. The fruit became edible after the first frosts in autumn. According to Kou Zongshi, writing in the *Bencao Yanyi* [Development of Herbal Medicine] (completed between 1111 and 1116 during the Song Dynasty), *mihoutao* were very common in the mountains of what is today parts of Gansu, Shaanxi, Shanxi, and Henan Provinces. The *mihoutao* supported themselves by climbing over trees, fruiting vines were often found along pathways in the hills, and in more remote areas, most of the fruit were eaten by monkeys. This consumption of fruit by monkeys gave rise to the name *mihoutao* [monkey peach]. Thus, in what is probably the best known of all Chinese pharmacopoeias, the *Bencao Gangmu* [Great Compendium of Herbal Materia Medica] (1590, Ming Dynasty), Li Shizhen said of the *mihoutao*, ". . . *its shape is that of a pear, its color that of a peach and monkeys like to eat it, hence its name.*" He described the leaves as being the size of a hand, green on the upper surface, white and hairy underneath. Subsequently in 1848 (Qing Dynasty), Wu Qijun in the *Zhiwu Mingshi Tukao* [Illustrated Account of Flora], recorded that the *mihoutao* was found in the mountains of Jiangxi, Hunan, Hubei, and Henan and that peasants took the fruit to towns and cities for sale.

There are, however, occasional other reports of cultivation. For the past several hundred years, villagers in Huangyan County, Zhejiang have transplanted wild *mihoutao* plants to grow them around their houses (Cui 1981; Ch'ang 1982; Qian and Yu 1992), with some of the existing plants being more than 100 years old (Zhu 1983). This, however, seems an isolated attempt at cultivation, and Frank Meyer, the plant collector who traveled extensively throughout China early in the 20th century concluded that *A. chinensis* (which then included *A. deliciosa*) was not cultivated at all (Meyer 1911). As late as 1978, there was still less than one hectare of cultivated kiwifruit in China (Cui 1981).

We have found no evidence that *Actinidia* species were formerly cultivated in Japan or Korea for fruit production. Occasional plants may have been grown as ornamentals: e.g., there is one venerable 600-year-old male plant of *A. arguta* growing in the gardens of the Chang-duk Palace at Seoul, Korea. This plant has a massive trunk 70 cm in diameter and 100 m of main branches (Shim and Ha 1999). The specimens that Siebold used to describe *A. volubilis* (now considered to be synonymous with *A. polygama*) were collected from cultivated plants (Siebold and Zuccarini 1843; Lavallée 1885), not from the wild. There is also an early, illustrated report (Ito and Kaku 1883) of a plant of *A. arguta* (but incorrectly identified as *A. volubilis*) growing in the Botanical Gardens at Tokyo, Japan. Otherwise, the reports available indicate that fruit were simply collected from the wild (Ito and Kaku 1883; Georgeson 1891; Batchelor and Miyabe 1893).

B. Early Western Introductions of *Actinidia* Species

The early botanical taxonomic history of *Actinidia* is outlined in Section II.A. The specimens of *Actinidia callosa* on which the genus is based were collected by Nathaniel Wallich, in Nepal, in 1821 and the new genus was described in 1836 by Lindley.

The first *Actinidia* species to be cultivated outside their homelands seem to have been *A. arguta*, *A. polygama*, and *A. kolomikta*, with many of the earliest plants grown coming from Japan. However, European and North American horticulturists initially confused the three species (as well as *A. volubilis*, now treated as a synonym of *A. polygama*) and names were frequently applied incorrectly. Without good illustrations, the plants described often cannot be identified with any certainty and the confusion is now difficult to resolve.

Rehder (1927) indicated that *A. kolomikta* was introduced into cultivation about 1855, but the earliest definite reports we have so far found are those of Salomon (1869) from Würzburg, Germany and of Bretschneider (1898) who noted that it first flowered in cultivation at St Petersburg in 1869. An illustration of what was said to be *A. kolomikta* appeared several years later in Carrière (1872), but certain identification of the plant shown is not easy. Masters (1880) reported that *A. kolomikta* had been introduced to Britain from Yesso, Japan by Maries, who visited there in 1877, but the plant described (although not illustrated) seems more like *A. polygama*, as also indicated by the name "cat's medicine" given to it by Veitch (1906). A more reliable identification of mature plants of *A. kolomikta* appears to be that of Schondorff (1879). The first really convincing illustrations were much later, those in Rehder (1896) and André (1898).

There is even greater confusion about the initial cultivation of *A. arguta* and *A. polygama* (confusion compounded by use of the name *A. volubilis*). Carrière (1874) illustrated what was identified as *A. volubilis*, but was more likely to have been *A. arguta*. Another early record is that of Ellacombe (1879) who had what he thought were *A. kolomikta* and *A. polygama* growing in his Gloucestershire (England) garden. An illustration and description published subsequently (Hooker 1896) of the plant Canon Ellacombe considered to be *A. polygama* show convincingly that it was, in fact, *A. arguta*. Plants grown for many years in Germany (Lauche 1879; Bolle 1880) and in France (Lavallée 1885) as *A. polygama* or as *A. volubilis* likewise appear to have been *A. arguta*: if the anthers were described as black, then without doubt, the plant could not be *A. polygama* (or, for that matter, *A. kolomikta*). The plant described by Lavallée (1885) (and which we now recognize as being *A. arguta*) had been in cultivation from before 1870 (Anon. 1875): this may therefore be the earliest convincing record of *A. arguta* being cultivated in Europe. What appears, from the detailed description, to have been the true *A. arguta* was introduced from Japan as cuttings into the United States in 1876 (Penhallow 1884) and, together with *A. polygama*, again introduced from Japan, was being grown in New England by the last decade of the 19th century (Orpet 1892; Anon. 1893, 1895). Within a few years, other *Actinidia* species had been introduced into cultivation in both Europe and the United States, largely as a result of the collecting trips of E. H. Wilson.

C. Domestication and Commercialization of *A. arguta, A. kolomikta, and A. polygama*

Initially *Actinidia* species seem to have been valued in Europe primarily as ornamentals, partly because many of the first plants were males or were females unaccompanied by males. However, reports from Asia, especially Japan, indicated that the fruit of some *Actinidia* species were very palatable.

The fruit of *A. kolomikta*, "little kishmish," although small, are very sweet, and were traditionally collected by the residents of Siberia and other areas where the species grows naturally. When the species was first grown in western Russia or in Europe, the sweet fruit, with a flavor reminiscent of pineapples, were soon recognized as being one of the main attractions. Graebener (1894, 1895) thought that *A. kolomikta* had great economic potential and he extolled it as a "Planze der Zukunft"—a plant of the future. There was also the advantage that the plant was very cold-tolerant and could crop at latitudes at which few other fruit-bearing plants even survive (Evreinoff 1949; Poyarkova 1949). I. V. Michurin introduced seed from Primorski Krai in 1910 and the first fruit were produced in 1915 (Titlyanov 1963). However, attempts to cultivate *A. kolomikta* in Russia or elsewhere have been largely unsuccessful despite the selection of larger fruited strains and hybrids superior to the wild plants (Evreinoff 1934, 1949; Michurin 1949). It seems that the small fruit, which do not store particularly well, cannot compete with other berry fruits in the marketplace and *A. kolomikta* has remained an ornamental or a plant for hobbyists, not for commercial production.

Reports from Asia also indicated that the fruit of *A. arguta* (sometimes misidentified as *A. volubilis*) were edible and had long been collected from the wild, whereas the unripe fruit of *A. polygama* were "extremely acrid" (e.g., Ito and Kaku 1883; Georgeson 1891; Batchelor and Miyabe

1893). The initial confusion in Japan and later in Europe as to which plants the names *A. arguta* and *A. polygama* should be applied meant that early reports on the palatability of the fruit of these species were understandably contradictory. Nevertheless, by the end of the 19th century it was generally accepted that the fruit of *A. arguta* ("large kishmish") were sweet and could have a very good flavor, even if somewhat astringent and "mildly purgative," whereas those of *A. polygama* were very pungent or peppery when unripe, and rather insipid when ripe.

In North America there was considerable emphasis on the potential of *Actinidia* as fruiting plants. Thus, as early as 1883, Penhallow (1884) was recommending *A. arguta* as a promising fruiting plant for North America, one that could be much improved by cultivation. Some European writers still had doubts, concluding that if the Japanese, renowned as such intelligent horticulturists, had not attempted to cultivate *A. arguta*, it was probably not worthwhile (Leichtlin 1895). Fairchild (1913) described the fruit of *A. arguta* as being very sweet, with a flavor reminiscent of figs, but commented that the long time required for the plant to reach sexual maturity and the need for both male and female plants discouraged wider cultivation. There was a need for expensive support structures and the vines were difficult to manage (Evreinoff 1934). Although *A. arguta* is very resistant to winter cold, it breaks bud and flowers early in the season. Furthermore, the fruit do not generally store well.

The commercial potential of *A. arguta* was often mentioned by subsequent American authors (e.g., Darrow and Yerkes 1937), but little real interest was shown until commercial plantings were recently established in Oregon, USA (Finn 1999). At present there are about 40 ha *A. arguta* orchards in Oregon, and about 15 ha in other states (Strik 2002). In New Zealand, there are about 40 ha planted (M. H. Williams, person. commun.) and small and occasional commercial plantings in Chile, France, Germany, Italy (Cossio and Telch 1989), and Japan (Sanada and Sato 2003; Okamoto and Goto 2005). There has also been recent interest in Canada in the potential of *A. arguta* for commercial production (Kabaluk et al. 1997).

Actinidia arguta remains a plant of possibly great potential but, with a few exceptions, is still limited mainly to hobbyists in areas that are too cold for the cultivation of other kiwifruit (Rusterholz and Husistein 2000).

There is restricted cultivation (2 ha) of *A. polygama* in Japan, with the fruit being used to make wine as they are not palatable when fresh (Sanada and Sato 2003). Fruit are also collected from the wild and more extensive cultivation of *A. polygama* is unlikely.

D. Domestication and Commercialization of *A. chinensis* and *A. deliciosa*

1. First Botanical Specimens. The earliest known botanical specimens of *A. chinensis* were collected by Incarville at Macao in late 1740, but these were not examined until about 150 years later (Franchet 1882). Instead, the specimens of a male plant in flower that were used to describe the new species, *A. chinensis* (Planchon 1847), were probably collected close to Ningbo, south of Shanghai, by Fortune in 1845 (Ferguson 1990b). The first fruiting specimens seem to be those of Henry, collected near Ichang (Yichang), Hubei and sent to Kew in 1886. These were used to prepare the first European illustration of the fruit published by Oliver (1887). The fruit shown are essentially hairless and appear to have only a scattering of hairs at the distal end of the fruit. These specimens, and some other early specimens collected in eastern China, all represent *A. chinensis* (*sensu stricta*); subsequent specimens collected in Sichuan and other parts of western China are of plants with much hairier fruit (Veitch 1904; E. H. Wilson, quoted Dunn 1911; Sprague 1914), plants that would now be placed in *A. deliciosa*. The nomenclatural and taxonomic history of *A. chinensis* (*sensu lato* and *sensu stricta*) and of *A. deliciosa* is detailed in Ferguson (1990b). In summary, the first botanical specimens and the first published botanical illustration of the fruit were of *A. chinensis* as now defined; many of the later botanical specimens collected for European and North American herbaria and almost all the published illustrations of the flowers and subsequent illustrations of the fruit were of what we now classify as *A. deliciosa*. Plants of both *A. chinensis* and *A. deliciosa* were being cultivated outside of China during the first years of the 20th century but it seems that only those of *A. deliciosa* survived and these became the basis of the worldwide kiwifruit industry (Ferguson 2004; Ferguson and Bollard 1990).

2. Introduction of *A. deliciosa* into Cultivation. The first known plant (or possibly plants) of *A. deliciosa* to be grown outside China was that listed as *A. chinensis* in the catalogue of the Arboretum of Maurice de Vilmorin in France (Vilmorin and Bois 1904). This was raised in 1899 from seed collected in 1898 and sent to France by the French missionary, Père Farges. At that time, Farges was stationed in northeast Sichuan (Bretschneider 1898), a location that indicates that the plant was most likely *A. deliciosa* not *A. chinensis*. This may have been a single plant and its eventual fate is not known.

The successful introduction of *A. deliciosa* into cultivation outside China is largely due to the efforts of the plant explorer, E. H. Wilson (Ferguson 1983; Ferguson and Bollard 1990; Ferguson 2004). Wilson was sent to China in 1899 by James Veitch & Sons, London to collect plants that would be suitable for the gardens of Europe and North America. On the first and second of his trips to China he was responsible for the first introductions of *A. deliciosa* (then included under the name *A. chinensis*) to Great Britain; he provided seed and plants that were sent to the United States Department of Agriculture; and he probably also provided the seed that went to New Zealand (Ferguson 2004).

The seed of *A. deliciosa* that Wilson sent to Britain in 1900 were successfully germinated and young plants were offered for sale in 1904. When they flowered, all these first plants proved to be male and fruit were not produced until 1911, after further introductions of seed collected by Wilson in China. Female plants of *A. chinensis* were first advertised for sale in Britain by James Veitch & Sons in 1912. Plants were sent from James Veitch & Sons to Europe, where male plants were recorded as flowering in 1909, but it seems that few fruit were produced there before 1937 (Ferguson and Bollard 1990). The potential of *A. deliciosa* as a fruiting plant had initially been much discussed (e.g., Wilson 1909), but eventually seems to have been forgotten: within Britain and Europe, *A. deliciosa* came to be generally considered as an ornamental climber that, as a bonus, sometimes produced fruit.

Wilson was also ultimately responsible for the initial introduction of *A. deliciosa* to the United States. In 1900, he gave fruit to the European residents at Ichang (Wilson 1913), the town at which he over-wintered in China, and from there seed were sent back by plant collectors working for the United States Department of Agriculture (USDA) (Ferguson 2004). Wilson also provided plants, originally obtained on the borders of Yunnan, which at great expense and with much effort were shipped to California. They arrived in July 1904. Two separate introductions, ". . . possibly distinct . . . ," were listed: P.I. No. (Plant Introduction Number) 11629 and P.I. No. 11630 (USDA 1907a), but four plants were mentioned when a photograph of the first flowers produced at Chico was published (USDA [1910?]). Cuttings were raised of these plants and Fairchild (1913) stated that by 1913 more than 1300 plants of *A. chinensis* (and/or *A. deliciosa*) had been distributed. However, there are some inconsistencies in the data and the USDA records indicate possibly only 56 locations to which P.I. No. 11629 had been sent. This plant, as well as the others obtained from Wilson, proved to be male so many of the initial plants distributed were useful only as ornamentals. Plants that were known to be female were finally imported in 1913, propagated from the plant that had produced fruit at the Veitch nursery in England (P.I. No. 35133, USDA 1915a), and a single first fruit was produced in the United States in 1915 (USDA [1915b?]). The photograph published of this small but very hairy fruit shows it to be unequivocally of *A. deliciosa*, not *A. chinensis*. By 1932, the USDA had distributed plants of *A. chinensis* and/or *A. deliciosa* to more than 2500 locations, some of which were overseas, but had received back only three reports of plants successfully fruiting. It is likely that some of the plants originally distributed by the USDA are still surviving in the United States but with one known exception, they did not contribute to the kiwifruit industry that subsequently developed in California. That one exception is the 'California Male' or 'Chico Male' (Ferguson 1997): this originated as a seedling from the introduction P.I. No. 21781, *A. deliciosa* seed sent by Wilson from Ichang, China and received in 1908 (USDA 1909). This later became one of the most widely used pollenizers in California.

Wilson was probably also responsible indirectly for seed of *A. deliciosa* going to New Zealand in 1904. These seed accompanied a New Zealand schoolteacher who had been visiting her missionary sister in Ichang (Ferguson 2004). Plants were raised and it is known that at least one of these was fruiting by 1910—probably the first-ever fruit of *A. deliciosa* produced outside China. All the important New Zealand cultivars of *A. deliciosa*, including 'Hayward', can be traced back to one male and two female plants that are themselves traceable back to that 1904 introduction of seed. Other material of *A. deliciosa* may have been imported into New Zealand at about the same time (possibly from James Veitch & Sons, which would make it material originally collected by Wilson) but it is the 1904 introduction that led directly to the kiwifruit industry in New Zealand (Ferguson and Bollard 1990).

Scientists in New Zealand realized that the industry had an extraordinarily narrow genetic base and that it was essential to introduce more diversity. However, it was not until nearly 70 years later, in 1975, that further seed of *A. deliciosa* were imported into New Zealand from China (M. A. McNeilage, person. commun.). Subsequently, a much greater diversity of seed and budwood of *A. deliciosa* has been imported into New Zealand and other countries.

3. Commercialization of *A. deliciosa*. Most aspects of the subsequent development of the kiwifruit industry in New Zealand based on cultivars of *A. deliciosa* have been previously described in detail (Yerex and Haines 1983; Earp 1988, 1990; Ferguson and Bollard 1990; Warrington 1990; Webby 2004). Only some of the critical steps need therefore be summarized.

Plants Sold to the Public. Initially, plants were sold or exchanged between enthusiastic plantsmen and between nurserymen but by 1917, nurserymen in New Zealand were selling plants of *A. deliciosa* to the public. By 1924, the new plant was provoking much interest (Ferguson and Bollard 1990).

Grafted Plants. It is obvious that male kiwifruit flowers are inadequate for fruit production but female flowers appear misleadingly perfect and it took many years to realize that their pollen is not viable. The first known grafted plants of identified gender to be sold anywhere in the world were the female plants available from James Veitch & Sons in 1912 to accompany the male plants already available from previous introductions. Some of these female plants may have gone to New Zealand, but, if so, there is no evidence that they were ancestors of any of the kiwifruit cultivars selected there (Ferguson and Bollard 1990). Plants of known gender were being sold in New Zealand, possibly as early as 1922, definitely by 1926. Initially they were sold as grafted or budded plants but soon they were also produced from cuttings.

First Commercial Orchards. The possibility of fruit production had been considered long before kiwifruit had even been successfully brought into cultivation (e.g., Henry 1893). Once some plants had been successfully grown in the United States, the possibility of commercial orchards was again suggested (e.g., USDA 1922). The first known orchard to be actually established, however, was that in Wanganui, New Zealand, a small planting of some 14 vines which was producing good crops of fruit by the early 1930s. Fruit were soon being shipped to other towns in New Zealand for sale. Before long, further plantings followed in other parts of New Zealand, mainly in the Bay of Plenty. These initial orchards were likewise all small and generally less than 1 ha in area (Ferguson and Bollard 1990; Webby 2004).

Cultivar Selection. Vegetative propagation meant that it was sensible to propagate only those forms that had better quality fruit. Two New Zealand nurserymen, Hayward Wright and Bruno Just, selected most of the forms most widely planted but for many years there was still great confusion, as a good form might carry several different names or be renamed according to the source of propagation wood. Eventually, the best strains were identified and characterized, their origins determined, and they were given names commemorating some of the industry pioneers (Mouat 1958). Two of these cultivars are still commercially important: ‘Bruno’, named for Bruno Just, is grown extensively in China and

'Hayward', named for Hayward Wright, is the mainstay of the industry in most parts of the world.

Cold Storage. Kiwifruit were initially grown in New Zealand for the local market but the steady increase in the area planted eventually meant that there was an oversupply of fruit at the peak of the season. Although the fruit of some kiwifruit selections have a long shelf-life, growers started considering cold storage as a means of extending the season. Experimental storage trials established that kiwifruit could be stored at 0°C for extended periods, and that the state of maturity at which the fruit was harvested was important in determining its storage life and its quality when it came out of store. Growers quickly took up these results and in 1952 came the first commercial storage of kiwifruit with 4.2 t being successfully sold after prolonged cold storage. Within a few years, cold stores were being constructed mainly for kiwifruit (Ferguson and Bollard 1990).

The Start of International Trade. Export markets could also absorb surplus fruit if refrigerated ships were available. A trial shipment of kiwifruit was sent to Britain in 1952 and the first commercial shipment of about 12 t followed a year later. With increasing market acceptance and the stimulation of interest, rather than export markets absorbing surplus fruit, growers started producing kiwifruit specifically for export. The surge in plantings of kiwifruit in New Zealand from about 1973 was largely in response to the expansion of kiwifruit exports and the very good prices realized. Each year a greater proportion of the crop was exported and in 1976, exports of kiwifruit from New Zealand for the first time exceeded local consumption.

Marketing, the Predominance of 'Hayward' and the Change of Name. The expansion of markets in the United States, Europe, and Japan was due not only to the inherent qualities and attractiveness of kiwifruit; expansion was also helped by the successful marketing strategies of the New Zealand exporters and by sustained promotion. Kiwifruit came to be grown for export and the standards and the procedures adopted were designed to satisfy the overseas customers. It was accepted that the customers preferred 'Hayward' kiwifruit, largely because fruit of this cultivar could withstand prolonged storage so much better. Growers, therefore, converted existing kiwifruit orchards to 'Hayward' or planted only 'Hayward' when new orchards were established. By 1975, the predominance of 'Hayward' was essentially complete (Ferguson 1999b)—apart from the pollenizers, kiwifruit orchards became a monoculture of

'Hayward' vines and only 'Hayward' fruit were accepted for export. Even the old common name of "Chinese gooseberry" was discarded because of marketing strategies, to be replaced by the new-fangled "kiwifruit"—now the accepted name through the world.

Development of Kiwifruit Industries in Other Countries. The initial development of the kiwifruit industry in New Zealand and the cultivars used were based on the single importation of *A. deliciosa* seed in 1904. Inevitably, as other countries started growing kiwifruit in response to the success of the New Zealand industry, they too started growing *A. deliciosa* and likewise, they too adopted New Zealand cultivars because of their perceived superiority (Ferguson and Bollard 1990; Ferguson 1999a). Thus, the commercial plantings in Europe were founded on New Zealand cultivars as were those of Chile and California. The worldwide kiwifruit industry as it developed was based on that 1904 single introduction of seed (Ferguson and Bollard 1990).

4. Commercialization of *A. chinensis*. The first attempts to cultivate *A. chinensis* and *A. deliciosa* were made at about the same time, at the beginning of the 20th century. Introduction of *A. deliciosa* into cultivation was achieved within a few years, but that of *A. chinensis* took nearly another 60 years.

Introduction of A. chinensis *into Cultivation.* In 1905, seed of what was listed as *A. chinensis* were sent from China to the USDA. The seed (P.I. No. 18535) came from Kuling (now Lushan) Jiangxi, and the description (USDA 1907b) and a photograph (Fairchild 1927) of the fruit indicate that this seed was indeed of what we now classify as *A. chinensis*. Plants were raised and at least seven of these were distributed (unpublished information, United States Department of Agriculture, Bureau of Plant Industry, *Actinidia* File). This is the first unequivocal record of material of *A. chinensis* (*sensu stricta*) being sent out of China and of plants being successfully raised, even if the eventual fate of these plants is unknown. Other material of what was, from the geographic origins or the descriptions, almost certainly *A. chinensis*, was imported into the United States, e.g., P.I. No. 26904 (USDA 1911), P.I. No. 41401 (USDA 1918), P.I. No. 45946 (USDA 1922), and of the latter two accessions, plants were distributed to nearly 700 locations (Bureau of Plant Industry, USDA files), although all plants are now apparently lost without trace. Thus, these early attempts to introduce *A. chinensis* to the United States seem to have all been unsuccessful although it is possible that some plants still survive there. There is no evidence that any attempts were made to introduce the true *A. chinensis* into Europe or New

Zealand during the first part of the 20th century: certainly, we do not know of any plants surviving.

The successful introduction of *A. chinensis* into cultivation in China commencing in 1961 is considered in the following section. The first successful introduction of *A. chinensis* to a country outside of China was in 1977 when seed were brought from China to New Zealand through D. W. McKenzie of the New Zealand Department of Scientific and Industrial Research (M. A. McNeilage, person. commun.). A total of 43 plants were raised from the seed and planted out. Within a few years, the vines were producing large crops of fruit, almost certainly the first-ever fruit of this species outside of China. Some of these original vines are still maintained in the HortResearch *Actinidia* germplasm collection. As discussed later (Section V.A.5) there is a direct line of descent from the plants raised from this first accession of *A. chinensis* seed into New Zealand and the cultivar 'Hort16A'.

Since then there have been many more introductions of seed and budwood of *A. chinensis* into France, Italy, Japan, New Zealand, and the United States (e.g., Zuccherelli 1994; Testolin et al. 1999a; Blanchet and Chartier 1998; Ferguson and McNeilage 1999; Nicotra et al. 1999). Fruit of the Chinese cultivars 'Lushanxiang', 'Jiangxi 79-1', and 'Jinfeng' have been produced in southern California and sold on the Los Angeles market since 1995 (R. Meyer, person. commun.).

When the first plants of *A. chinensis* were grown outside of China, *A. chinensis* (s.s.) and *A. deliciosa* were still considered as varieties of the one species *A. chinensis*, and the comparative advantages and disadvantages of the two variants were not fully appreciated. It is now clear that there is greater diversity within *A. chinensis* than in *A. deliciosa* in attributes such as fruit flesh color and flavor.

Commercialization of A. chinensis *and* A. deliciosa *in China.* The success of kiwifruit, first in New Zealand, and then in other countries, stimulated Chinese interest in the potential of their wild *Actinidia* germplasm resources. The first serious attempt at cultivation started with the introduction of *A. deliciosa* to the Beijing Botanic Gardens, Institute of Botany, Academia Sinica, in 1957 using seed from Mt Zhongnan, Qinling Mountains, Shaanxi (Zhang et al. 1983; Huang et al. 2003). This introduction can be considered as the start of the systematic evaluation of *A. deliciosa* as a crop plant in China, even if these early studies did not result in development of commercial cultivars. Beijing is well north of the natural range of *A. deliciosa*, but plants were successfully grown and fruit produced by taking precautions against winter and spring cold.

In 1958, the Central China Agricultural College started a germplasm survey and selection of superior genotypes in Wudangshan Mountains of Hubei and in 1961, the Institute of Botany likewise started growing *A. chinensis* in the Beijing Botanic Gardens using seed from fruit collected near Neixiang in the Funiu Mountains, Henan (Zhang et al. 1983; Huang et al. 2003, 2004). This small plantation in Beijing is historically important as it can be considered as the start of the modern domestication of *A. chinensis*. The Botanic Gardens also subsequently introduced plants of *A. arguta*, *A. kolomikta*, and *A. polygama* into cultivation.

Many of the first commercial orchards in China used *A. deliciosa* cultivars from New Zealand. However, in late 1977 and early 1978, evaluation of the natural resources of *Actinidia* in China was made more systematic with the establishment of Mihoutao Keyan Xiezuo Zu (the Chinese National Co-operative Group for Kiwifruit Research) with the role of encouraging surveys of wild germplasm of all *Actinidia* species, particularly *A. chinensis* and *A. deliciosa*, and the selection of superior genotypes for cultivar development to replace the cultivar ‘Hayward’ imported from New Zealand. More than 1400 promising individuals were selected for further study (Qian and Yu 1992) and several hundred were named on evaluation after grafting, regional tests, and replicated trials. Many of the more promising of the *A. chinensis* and *A. deliciosa* selections are now in commercial cultivation (Huang and Ferguson 2001, 2003; see also Table 1.6, Section V). The most successful of these would be ‘Qinmei’, the second most widely planted of all *A. deliciosa* cultivars with a current total area in China of about 20,000 ha.

Commercialization of A. chinensis *outside China.* At present, only one *A. chinensis* cultivar is being cropped on a commercial scale outside of China. This is the cultivar ‘Hort16A’, first grown in New Zealand and now being grown under licence in countries such as France, Italy, and Japan to ensure year-round supplies for marketing. The entry of ‘Hort16A’ fruit, or yellow-fleshed kiwifruit, into the international marketplace is probably the biggest change to kiwifruit marketing since kiwifruit exports from New Zealand were restricted to the cultivar ‘Hayward’. Long-term, this change is likely to prove more fundamental than the transition from New Zealand being the sole producer of kiwifruit to being only one of the producers of kiwifruit, not even the biggest producer. In the eyes of retailers and consumers worldwide, kiwifruit have gone from being a single fruit, ‘Hayward’, to two complementary types of fruit and it is likely that other, perhaps more competitive, cultivars may soon start emerging. Already, plantings of other yellow-fleshed cultivars of *A. chinensis* have been established in Europe.

E. The World Kiwifruit Industry

Actinidia chinensis and *A. deliciosa* are at present the only two *Actinidia* species of commercial importance. To most consumers, the fruit of these two species would appear to be very similar and in the marketplace they are grouped together as kiwifruit (UNECE Standard for Kiwifruit FFV-46).

1. World Plantings of Kiwifruit. The total area in kiwifruit orchards (*A. chinensis* and *A. deliciosa*) throughout the world is currently about 120,000 ha. In 2004, China had 65,000 ha of kiwifruit orchards, Italy approximately 21,000 ha, New Zealand 11,500 ha, Chile 8000 ha and all other countries (mainly Iran, France, Greece, Japan, and USA in decreasing importance) a total of about 20,000 ha (Belrose Inc 2005; unpublished statistics from the Chinese National Cooperative Group for Kiwifruit Research). Over the past decade, kiwifruit plantings have remained comparatively stable in many countries such as Italy and New Zealand, there have been declines in California, Chile, Greece, and Japan and a proportionately big increase in Iran, although the area there is still a small part of the world total. The most significant change has been the dramatic increase in Chinese kiwifruit orchards. In 1978, China had less than 1 ha of cultivated kiwifruit; by 1990 the total kiwifruit plantings in China had increased to 4000 ha; by 1996 to 40,000 ha; by 2002 to more than 57,000 ha (Huang and Ferguson 2001, 2003); by 2003 to 61,500 ha and in 2004 to 64,700 ha. Half of the world kiwifruit orchards are now in China. A single province in China, Shaanxi, has a greater area planted in kiwifruit than does New Zealand, until recently the world's largest producer of commercial kiwifruit.

2. World Production of Kiwifruit. In 2004, total world production of commercial kiwifruit (both species) was approximately 1,500,000 t. This estimate is based on figures from the International Kiwifruit Organization (R. A. Martin, person. commun.) and the Chinese National Cooperative Group for Kiwifruit Research. China produced 400,000 t, about the same as Italy, New Zealand 280,000 t, and Chile 120 to 150,000 t so together, these four countries accounted for about 80% of world commercial kiwifruit production and other countries are generally becoming less important. Yields in any particular season can be affected by weather so over the past decade total production in both New Zealand and Italy has fluctuated around a general upward trend and that in Chile seems to have stabilized (Belrose Inc 2005). However, consideration of only the total kiwifruit plantings and production in New Zealand is misleading because it obscures the conversion of existing 'Hayward' orchards to 'Hort16A'. Exports of 'Hort16A' fruit now account for about 20% of the total New Zealand exports of kiwifruit.

The most significant change over recent years has been the greatly increased production by China following the earlier surge in plantings. In 1990, the total production from Chinese commercial kiwifruit orchards was estimated to be about only 5000 t, an insignificant quantity, so the increase since then is most impressive and dwarfs the changes in production of other countries (Huang and Ferguson 2001, 2003). For the most recent period for which we have consistently based estimates, 1998–2004, total commercial production of kiwifruit in China is thought to have increased more than three-fold from 118,500 to 402,700 t.

China could soon be producing more kiwifruit from commercial orchards than any other country. Most of its kiwifruit orchards are still young and many of the vines have not yet achieved mature cropping; yields per hectare are still much lower than in many other countries. Although the statistics for China are based on expert estimates, there can be no doubt of the trend, no doubt that the importance of China in the world kiwifruit industry has increased dramatically over the last decade. Furthermore, considerable quantities of kiwifruit are still harvested from the wild in China, between 100,000 and 150,000 t per year (Huang and Ferguson 2001; Chen 2003), even if these wild fruit are likely to become less important as commercial production continues to increase.

3. Important Cultivars of *A. chinensis* and *A. deliciosa* in International Trade. The kiwifruit industry in New Zealand was originally based on cultivars of *A. deliciosa* and, since about 1975, on 'Hayward', one single fruiting cultivar of that species. International world trade in kiwifruit is still dominated by fruit of 'Hayward', accounting for perhaps 95% of all kiwifruit traded. Such reliance of an industry on a single cultivar in most parts of the world is unusual. Other cultivars of *A. deliciosa* have been planted on a small scale, e.g., Top Star® in Italy and 'Tomua' in New Zealand, but the amount of fruit from these is insignificant in terms of trade and 'Tomua' is no longer grown commercially. Other new cultivars of *A. deliciosa* are being planted, e.g., Summerkiwi™ in Italy, but as they are not yet in mature production their likely potential cannot be assessed.

The rise in Chinese kiwifruit plantings is resulting in changes in the overall species and cultivar composition of kiwifruit orchards throughout the world. In China, 24% of current commercial kiwifruit plantings are of *A. chinensis*, 67% are of *A. deliciosa*, with the remaining 8.5% unspecified as to species (Huang and Ferguson 2003). Outside of China, plantings and production are almost entirely of *A. deliciosa*, and the area in *A. chinensis* would at present amount to little more than another 3000 ha at most (c. 5% of the total kiwifruit plantings outside China). Thus, of the total area planted in kiwifruit throughout the world (including China), about 15% is in *A. chinensis*, 85% in *A. deliciosa*.

The only significant quantity of *A. chinensis* fruit currently produced outside China is of 'Hort16A' (sold as ZESPRI™ GOLD Kiwifruit): 27,000 t were exported from New Zealand in 2002, 31,000 t in 2003, more than 50,000 t in 2004. These exports in the 2004 season accounted for nearly 20% of all kiwifruit exported from New Zealand that year. They would therefore amount to perhaps 6 to 7% of international trade in kiwifruit. However, most 'Hort16A' orchards are still young and not fully cropping and new plantings are still being established, particularly outside New Zealand to ensure 12-month supplies.

Another *A. chinensis* cultivar with yellow-fleshed fruit is 'Jintao'. This was developed in China but was first commercialized in Europe with c. 300 ha planted recently in Italy (Testolin 2001; Huang et al. 2002b; Consorzio kiwigold® 2002). Currently, the quantity of 'Jintao' fruit produced is insignificant in terms of the total Italian production of kiwifruit, but the Conzorzio kiwigold® hopes that within the next decade production of 'Jintao' fruit could increase to about 30,000t. 'Jintao' is being enthusiastically promoted under the slogan "The third millennium kiwi fruit from China" and plantings have been established in Chile for year-round supplies.

4. Cultivars of *A. chinensis* and *A. deliciosa* in China. Three of the four main kiwifruit producing countries are reliant on exports. New Zealand has a particularly small home market and 90% of its kiwifruit are exported each year; Chile and Italy each export c. 75% of the kiwifruit they produce, although Italy does also import about one third of its requirements because of seasonal market demands. These industries were based on 'Hayward' although subsequently, New Zealand diversified with the development of 'Hort16A'. In contrast, the Chinese kiwifruit industry has evolved almost entirely to satisfy local demand and, up to now, there has been only very limited export of the fruit produced. Thus, China has not been under the same pressure to standardize on 1 or 2 cultivars. Instead kiwifruit plantings in China are striking for their much greater diversity (Table 1.6): the 3 main cultivars make up less than 60% of the total area in kiwifruit; a further 4 cultivars of *A. deliciosa* and 7 of *A. chinensis* together account for only another 28% of the area in kiwifruit. Most of these cultivars are not widely known elsewhere and this could hinder the development of exports from China, irrespective of fruit quality. Generally, a particular cultivar is restricted to one or two provinces and there often seems to be a strong preference

Table 1.6. Main Chinese kiwifruit plantings by species and by cultivar, 2004. Data were collated at the Annual Meeting of the *Actinidia* Section, Chinese Society for Horticultural Science, Shishou, Hunan, 18–20 October 2004. Total area in China planted in kiwifruit, 64,500 ha.

Cultivar	Area (ha)	% total planted area in China	Most important areas
ACTINIDIA CHINENSIS			
Hongyang	3,000	4.7	mainly Sichuan, also Shaanxi, Henan
Zaoxian	2,700	4.2	Zhejiang, Jiangxi, Anhui
Kuimi	2,050	3.2	Zhejiang, Anhui
Jinfeng	1,950	3.0	Zhejiang, Fujian, Jiangxi
Wuzhi No. 3	1,400	2.1	Hubei
Guihai No. 4	675	1.0	Guangxi
Lushanxiang	675	1.0	Fujian, Jiangxi
ACTINIDIA DELICIOSA			
Qinmei	20,000	31.0	mainly Shaanxi, also Henan, Guizhou
Hayward	9,490	14.7	Sichuan and Guizhou, also Shaanxi, Anhui, Hubei
Miliang No. 1	8,460	13.1	Guizhou, Hunan, Zhejiang, Fujian
Jinkui	2,900	4.5	Jiangxi, Fujian, Hubei, Anhui
Bruno	2,300	3.6	Zhejiang
Chuanmi No. 1	1,300	2.0	Sichuan
Xuxiang	1,070	1.7	Jiangsu, Zhejiang, Hubei

for local selections. There is a need to restrict plantings to those cultivars with better quality fruit (Zhao et al. 2003).

The *A. deliciosa* cultivar ‘Qinmei’ is by far the most widely planted but still accounts (with its associated pollenizers) for little more than 30% of the total plantings in China, ‘Hayward’ and ‘Miliang No. 1’ each occupy about 15% of the area but no other cultivar accounts for even 10% of the total area. Although kiwifruit have their origin in China, two *A. deliciosa* cultivars of New Zealand origin, ‘Bruno’ and ‘Hayward’, now make up about one fifth of the Chinese area in kiwifruit: ‘Bruno’ because it is very productive and tends to be more amenable to different management techniques; ‘Hayward’, because of its superior flavor and long storage life.

No one cultivar of *A. chinensis* predominates or accounts for more than 5 to 6% of the total kiwifruit plantings in China (Huang and Ferguson 2001, 2003). These cultivars are restricted to China, except for experimental plantings in other countries and a small commercial orchard in the United States.

5. Segmentation of the Kiwifruit Market by Fruit Flesh Color. Not all kiwifruit have green-fleshed fruit and the kiwifruit market can be segmented according to fruit flesh color (Ferguson 2003; Zambujo 2003). Fruit of all *A. deliciosa* so far examined do have green flesh varying only in intensity of color. The only exceptions are very occasional mutants, e.g., 'Goldy', whose fruit apparently do not contain chlorophyll. Some genotypes of *A. chinensis* also have green-fleshed fruit when ripe (e.g., 'Wuzhi No. 3'), but most have fruit ranging in color from lime-green to yellow, the actual shade depending on the maturity of the fruit. A few, for example, 'Jinfeng', have fruit whose flesh is a spectacular golden yellow when ripe. On the basis of fruit flesh colour, nearly 90% of kiwifruit produced anywhere in the world (both *A. chinensis* and *A. deliciosa*) have green flesh, the remainder yellow flesh (all *A. chinensis*). Considering only kiwifruit production outside of China, about 5% of fruit produced have yellow flesh. So far, 'Hort16A' is the only yellow-fleshed *A. chinensis* cultivar outside China produced in significant amounts, but this is changing with the commercialization of yellow-fleshed cultivars such as 'Jintao' and ChinaBelle® (Blanchet et al. 1999). The difference in appearance between green-fleshed cultivars such as 'Hayward' and yellow-fleshed cultivars such as 'Hort16A' is very striking and far more obvious to the consumer than other differences between the fruit of the species *A. chinensis* and *A. deliciosa*, except perhaps skin hairiness. Flesh color is the basis of the ZESPRI™ segmentation of the kiwifruit market with the branding of ZESPRI™ GREEN Kiwifruit (at present, 'Hayward') and ZESPRI™ GOLD Kiwifruit ('Hort16A'). The flavor of 'Hort16A' is very different to that of the traditional green 'Hayward' and aggressive marketing may result in consumers associating certain types of flavor with different flesh colors.

Some kiwifruit, classified as *A. chinensis* var. *rufopulpa* and as *A. deliciosa* var. *coloris* have a central band of red flesh around the core, the band varying in intensity, width and anthocyanin composition. One of the most spectacular is the *A. chinensis* cultivar 'Hongyang' [Red Sun] (Wang et al. 2003). About 3000 ha of this cultivar have been planted, mainly in Sichuan, and it is now the most widely planted of all selections of *A. chinensis* in China (Table 1.6). However, most vines are still young and exports of the fruit out of China are still limited.

V. ORIGINS OF KIWIFRUIT CULTIVARS

A. Cultivars of *A. chinensis* and *A. deliciosa*

1. Selection from the Wild. Nearly all the cultivars of *A. chinensis* and *A. deliciosa* currently grown in China are selections from the wild (Huang 1999). Budwood was collected from plants that were identified as promising and was then grafted or propagated. Thus 'Qinmei', the most widely planted kiwifruit cultivar in China, was selected from the wild in Zhouzhi County, Shaanxi; 'Miliang No. 1', the next most important of Chinese selections of *A. deliciosa*, was likewise selected from the wild near the town of Miliang, Fenghuang County, Hunan. With one exception (*A. deliciosa* 'Jinkui'), the current leading Chinese kiwifruit cultivars listed in Huang and Ferguson (2001) all originated in the wild; nearly all the 35 cultivars of *A. chinensis* and *A. deliciosa* listed in Cui et al. (2002) are likewise described as being selected from the wild; similarly, 37 of the 42 Chinese cultivars of *A. chinensis* and *A. deliciosa* studied by Zhen et al. (2004) were wild selections. Many of the better *A. chinensis* selections are tetraploids and come from the Mufu Shan, mountains between Hubei and Jiangxi (Xiong 1992). A promising red-fleshed selection of *A. chinensis*, 'Chuhong', was likewise collected from the wild in Hunan (Wang et al. 2004), and a red-fleshed selection of *A. deliciosa*, 'Hongmei', from the mountains of northern Sichuan (Wang et al. 2005).

Most of these various selections were identified during a coordinated program which started in 1978 and involved many national and provincial Chinese research organizations and universities (Huang et al. 2003). The current wide range of kiwifruit cultivars available in China represents the culmination of an unusually comprehensive and systematic sampling and evaluation of the wild germplasm. The genetic base of the kiwifruit industry in China is, therefore, much broader than for kiwifruit industries in other countries.

Some of the Chinese kiwifruit cultivars originally collected from the wild are now being considered for commercial cultivation outside China, e.g., the yellow-fleshed *A. chinensis* cultivar 'Jintao', recently commercialized in Europe, was initially selected from wild vines in Wuning County, Jiangxi (Huang et al. 2002b). 'Jintao' seems to adapt well to different climates and produces large fruit with a good flavor and extended storage and shelf life.

2. Seedling Selections. In some cases, seed was collected from the wild and the more promising of the seedlings were selected or seedlings themselves were collected from the wild. The Chinese *A. chinensis* selections 'Guifeng', 'Guilu', 'Guimi', and 'Xuzhou 78-3' appear to have originated in this way (Cui et al. 2002). The red-fleshed cultivar 'Hongyang' was selected from 3213 seedlings raised from seed of fruit of *A. chinensis* var. *rufopulpa* collected in the wild in Henan Province (Wu and Li 1993; Wang et al. 2003). The French cultivars of *A. chinensis*, ChinaBelle® and its pollenizer PolliChina®, were also selected from plants grown from seed collected in the wild (Blanchet and Chartier 1998).

The 'California Male' or 'Chico Male' is the only *A. deliciosa* cultivar grown outside China that is recorded as having originated directly from seed collected in the wild (see Section IV.D.2). Most of the *A. deliciosa* cultivars developed in New Zealand, such as 'Abbott', 'Allison', 'Bruno', 'Gracie', 'Hayward', and 'Monty', are also seedling selections, but at least one generation removed from the original introduction of seed to New Zealand (Ferguson 1997). Thus 'Hayward' was a selection from a row of 20, possibly 40 seedlings from which the cultivar 'Gracie' was also selected. All these old cultivars seem ultimately to be derived from one male and two female plants which may have arisen directly from the original introduction of seed to New Zealand or are descendants of the first plants (Ferguson and Bollard 1990). The corresponding males were also seedling selections, but their origins are unclear.

A number of *A. deliciosa* cultivars have arisen as selections from open-pollinated seedlings of named cultivars or selections. The most prominent example is 'Jinkui', the third most widely planted of Chinese *A. deliciosa* cultivars. It is only one generation from the wild, being a selection in Hubei from thousands of open-pollinated seedlings of 'Zhuxi No. 2', itself a selection from the wild (Cui et al. 2002; Chen 2003). Other examples have arisen as open-pollinated seedlings of 'Hayward', e.g., 'Koryoku' (Japanese Plant Patent No. 1446), 'Tewi', and 'Vincent' (Ferguson 1997) or the Chinese selections 'Shixuan No. 3', 'Xianglv', 'Xuguan', and 'Xuxiang' (Cui et al. 2002; Chen 2003; Zhen et al. 2004). MontCap® is a second generation seedling from open-pollination of 'Hayward' (Blanchet 1995).

The origin of some seedlings is not specified and probably cannot now be determined. Although they have been identified in various parts of the world, it is likely that, apart from those in China, they all resulted from open-pollination of cultivars from New Zealand and are hence, ultimately derived from the original introduction of seed into New Zealand. Such cultivars include 'Brodie', New Zealand (Anon. 1987), 'Donné', South Africa (Linsley-Noakes 1990), and 'Saanichton 12', Canada. 'Blake', California (Meyer 1987) is possibly derived from separate early introductions of *A. deliciosa* into California.

3. Clonal Selections. Numerous clonal selections have been made of *A. deliciosa* 'Hayward' but the distinctiveness or the superiority of most of these clones is not at all clear. They were usually chosen as having fewer fruit faults such as excessive width or frequent 'Hayward' mark. Examples would include 'Hayward' Clone 8 (Testolin et al. 1994), 'Hayward' Clone K, and 'Hayward' Clone Maeba® (Valmori 1991), all from Italy, and 'Hayward Kramer' Clone from New Zealand (Ferguson 1997).

4. Budsports or Mutations. Some kiwifruit budsports have commercial potential. 'Wilkins Super' is a budsport of 'Hayward' first noted and collected in New Zealand in 1979 (US Patent 4,686,318). It has large fruit, longer and more cylindrical than those of 'Hayward'. TopStar® is a bud mutation of 'Hayward' originating in 1985 near Verona, Italy (Bergamini 1991). Its fruit are very similar to those of 'Hayward' but are essentially hairless. Green Light® is another sport of 'Hayward', collected at Brisighella, Italy, and promoted because the fruit mature about a month ahead of 'Hayward' (Anon. 2003). 'Wancui' is a sport of 'Hayward' collected in China (Zhu and Ding 2003).

Several large-fruited budsports of *A. chinensis* 'Hort16A' have been detected because a cane or even a whole vine has consistently larger fruit, sometimes almost twice the weight of those on neighboring canes or other vines (Martin 2005). These budsports may have potential either in their own right or as parents in breeding programs.

Other budsports, such as those giving rise to gender variants (Section II.C), are not of immediate commercial value but could also be very useful in breeding programs.

5. Selections from Controlled Crosses. Comparatively few successful cultivars have so far resulted from controlled, planned crosses. The breeding methods used are described in Ferguson et al. (1996); Marsh et al. (1999); Seal (2003); and Oliveira and Fraser (2005).

'Tomua' was a seedling from a cross made in New Zealand between 'Hayward' and an early flowering male from an accession of *A. deliciosa* seed from China (Muggleston et al. 1998). The intention was to produce a fruit that could be harvested well before 'Hayward'. 'Tomua' has large fruit, similar in many respects to those of 'Hayward', but maturing 2 to 4 weeks earlier. Although the fruit have a good flavor, the industry was unable to handle them satisfactorily and the cultivar is no longer grown commercially. Other *A. deliciosa* cultivars originating from controlled crosses include 'Katiuscia', 'Silvia', and 'Stefania' from Italy (Valmori 1991) and 'Skelton' from New Zealand (US Plant Patent PP 8,334), but none of these has been widely grown. More interest is currently being shown in two *A. deliciosa* Summerkiwi™ selections from Italy that arose from pollination of 'Hayward' by a fruiting male. 'Summer 4605' is reported to mature 4 to 6 weeks ahead of 'Hayward' (Ossani 2002b; Testolin 2005) and 'Summer 3373' 7 to 8 weeks ahead of 'Hayward' (Ossani 2002a; Testolin 2005).

The most successful product of planned, controlled crosses is the New Zealand *A. chinensis* cultivar 'Hort16A', the fruit of which are marketed under the name ZESPRI™ GOLD Kiwifruit. It resulted from a cross between a female derived from one accession of seed from China and a male derived from another, separate accession of seed from a different part of China. The female was chosen from open-pollinated seedlings of the first accession, i.e., one generation removed from the original introduction, because its fruit, although very small, had a good sweet flavor and attractive yellow fruit flesh, very different to the then usual green flesh of 'Hayward'. There was even a very small amount of red pigment around the central core of the fruit. The male was chosen because its female siblings all had large fruit. The aim was to combine fruit size, good flavor, and yellow flesh (Muggleston et al. 1998; Ferguson et al. 1999). The cross was made in 1987, the 'Hort16A' seedling first fruited in 1990, and it was selected for further assessment in 1991.

6. Pollenizer Selections. Most pollenizers have probably originated as seedlings in orchards or have been taken from the wild but a few are byproducts of breeding programs, e.g., *A. deliciosa* 'Ranger' and 'King' are siblings of 'Tomua'. Autari® (formerly 12.255) is a seedling of a cross between 'Hayward' and a fruiting male (Testolin et al. 1995c).

Pollenizers and the female cultivar grown must coincide in flowering time. 'Hayward' is consistently among the last of the female *A. deliciosa* cultivars to flower and the males chosen in New Zealand to coincide with it are not always suitable when it is being grown under different climatic conditions let alone for other female selections that flower earlier. Each new female cultivar usually requires distinct pollenizers to ensure optimum pollination. Tetraploid and diploid forms of *A. chinensis* flower about two and four weeks respectively before 'Hayward' and therefore require different pollenizers at the correct ploidy level to ensure seed viability.

In China, pollenizer selection has been largely ignored in most kiwifruit improvement programs. A notable exception is 'Moshan No. 4' developed at the Wuhan Institute of Botany (Wang et al. 2003). This pollenizer was originally selected in 1984 from the wild in Jiangxi province, an area from which many female cultivars such as 'Jintao', 'Wuzhi No. 2', 'Wuzhi No. 3', and 'Wuzhi No. 5' were also selected.

‘Moshan No. 4’ has become the pollenizer of choice for many fruiting Chinese kiwifruit cultivars because it has a long flowering period of 20 days and produces large amounts of pollen with high germination rates. It was the first kiwifruit pollenizer to be registered in China.

B. Cultivars of *A. arguta*, *A. kolomikta*, and *A. rufa*

There are many named selections of these three small-fruited species but the origins of most are not known. The earliest are those of Michurin (1949) and some are stated to be selections from the wild, whereas others appear to be the result of several cycles of crossing, possibly even hybrids between *A. arguta* and *A. kolomikta*. The genotypes that now carry the names of Michurin’s selections are not necessarily true to label. Chinese selections of *A. arguta* have been selected from the wild (Xiao 1999; Huang et al. 2003). Many of the selections available in Italy (Cossio and Telch 1989) or in North America are probably seedlings that were recognized, sometimes many years ago, as having good fruit (Strik and Cahn 2000). The four HortResearch *A. arguta* cultivars released by HortResearch, New Zealand, ‘Hortgem Tahi’, ‘Hortgem Toru’, ‘Hortgem Wha’, and ‘Hortgem Rua’, resulted from controlled crosses between different *A. arguta* accessions (Williams et al. 2003). These are now being commercialized.

C. Interspecific Crosses

The first recorded interspecific cross in *Actinidia* was that of Fairchild (1927) who crossed female *A. arguta* with pollen of *A. deliciosa*. The resulting plants, later called *A.* × *fairchildii*, had very small fruit and were of no commercial value. Since then many other interspecific crosses have been made with reasonable success (Wang et al. 1989, 1994; Ke et al. 1992; An et al. 1995; Cipriani et al. 1995; Chat et al. 1996, 1999; Hirsch et al. 2001) although successful fruit setting and seed formation can depend on the particular genotype combinations attempted (Harvey et al. 1992; Ferguson et al. 1996; Lee et al. 2004.). Very few of the plants produced, especially those resulting from wider crosses, have immediate merit but one interesting selection, ‘Kiri’, was produced from a cross *A. arguta* × *A. deliciosa* backcrossed to *A. deliciosa* (White and Beatson 1993). The fruit were large, averaging about 100 g and had a smooth edible skin, similar to that of *A. arguta*. The skin was however, easily damaged and the fruit had a short storage life. ‘Kosui’, released in Japan in 1999 is probably a hybrid of *A. chinensis* and *A. rufa*, ‘Shinzan’ an hybrid of *A. arguta* and *A. deliciosa*, and ‘Sanryoku’, a hybrid of *A. deliciosa* and *A. chinensis* (Kokudo et al. 2003). Hybrids between *A. deliciosa* and *A. arguta* and between *A. eriantha* and *A. chinensis* have also been selected in China (Xiao 1999).

Although none of the interspecific hybrids so far produced has been widely planted, they do show that the desirable characteristics of the fruit of different species can be assembled into novel packages. It will probably take several generations of backcrossing to achieve fully commercial selections.

Ornamental kiwifruit were a bonus from an interspecific breeding program initiated in 1983 at the Wuhan Institute of Botany with the aim of producing novel types of kiwifruit selecting for attributes such as high vitamin C content, long storage life, and ease of peeling. Two interspecific hybrid cultivars from the cross *A. chinensis* 'Wuzhi No. 3' × *A. eriantha* have been selected because of the number and attractiveness of the flowers they produced: 'Jianshanjiao' [Charming landscape] and 'Mantianxing' [Stars over the sky] (Wang et al. 2003). (For illustrations see Cui et al. 2002.)

VI. FROM GENETIC DIVERSITY TO CULTIVAR DEVELOPMENT

Kiwifruit were first discussed in *Horticultural Reviews* just over 20 years ago (Ferguson 1984). At that time, kiwifruit in New Zealand had just become important as a crop, important at least in New Zealand. The area of land occupied by kiwifruit orchards in New Zealand was probably much the same as today but total production was less than a third of that today. Kiwifruit cultivation was also just starting in other countries: in Chile the total plantings in 1984 were about 1000 ha and 200 t of fruit were produced; in Italy, in 1983, the area planted was 2500 ha and total production was about 9000 t (Warrington 1990). At that time, the total plantings in China were little more than 240 ha, largely of cultivars from New Zealand (Zhu 1983).

The dramatic development of the commercial industry has been paralleled by the increased knowledge and scientific understanding of the genus *Actinidia*. Twenty years ago, there was only a small number of scientists working full-time on kiwifruit and most publications referred to studies on a few *A. deliciosa* cultivars of New Zealand origin or was very old work describing some of the other species. Chinese information of *Actinidia* was either nonexistent or obtained outside of China only with great difficulty and sporadically. Today, the kiwifruit industry of China is becoming increasingly important and China is an acknowledged center of excellence for scientific studies on many aspects of kiwifruit biology. More than a quarter of the references we cite are by Chinese authors.

In this review we have attempted to consider most of the information available on genetic diversity within *Actinidia*. Even with only very limited sampling of the available germplasm resources, the variation is clearly enormous and the prospects for plant breeders are exciting. The more we know and the more we understand the basic biology of the genus, the better placed we will be to take advantage of that diversity. However, information on the diversity within the genus must be combined with conclusions as to what suits production and marketing (Seal 2003). Information on the likely response of marketers and retailers is essential as is information on the key factors that determine consumers' purchasing preferences, factors such as pleasure, convenience, and health (Ferguson 2003; Jaeger and Harker 2005). A knowledge of what is possible helps establish what is desirable in the ideal new kiwifruit. A clear goal is essential for any effective and efficient breeding program.

The breeding and selection of a new cultivar may be time consuming and expensive, but it is much more expensive to launch a new cultivar, to persuade orchardists to grow it, to persuade retailers to give it shelf space, and to persuade consumers to try it (Martin 2003). A full marketing and promotion package is required in each market. All these represent very significant investments, a total of between 10 and 12 times the cost of the original research to develop the cultivar (Martin and Luxton 2005). The identification of a plant with the ideal fruit characteristics is only the very first step in the development of a new commercial cultivar (Patterson et al. 2003).

The domestication of kiwifruit is a classic example of how wild plants are taken and made into commercial cultivated plants. Although the domestication of *A. deliciosa* started about a century ago, many of those who lead the rapid expansion and development of kiwifruit as a commercial crop are still alive today. The domestication of *A. chinensis* is even more recent and many of those involved are still active in research. The development of the kiwifruit industry worldwide continues.

LITERATURE CITED

Adorisio, S., M. Cappelloni, C. Lintas, and F. Monastra. 1990. Caratteristiche nutrizionali di frutti di actinidia prodotti in Italia. Riv. Frutticolt. Ortofloricolt. 52(10):61–65.

Alemán, A., J. Sastre, S. Quirce, M. de la Heras, J. Carnés, E. Fernández-Caldas, C. Pastor, A. B. Blázquez, F. Vivanco, and J. Cuesta-Herranz. 2004. Allergy to kiwi: A double-blind, placebo-controlled food challenge study in patients from a birch-free area. J. Allergy Clin. Immunol. 113:543–550.

An, H.-X., D.-R. Cai, X.-J. Mu, B. Zheng, and Q.-G. Shen. 1995. New germplasm of interspecific hybridisation in *Actinidia*. Acta Hort. Sin. 22:133–137.

André, E. 1898. *Actinidia kolomikta*. Rev. Hort. 70:36–37 + plate.

Anon. 1875. *Philadelphus* Souvenir de Billiard and *Actinidia volubilis*. The Garden 8(196):156.

Anon. 1893. Notes on trees and shrubs. *Actinidia arguta*. Am. Gardening 11(29):72.

Anon. 1895. The Editor visits Boston. Gardening (Chicago) 4(76):59.

Anon. 1987. New kiwifruit variety set for star status. Comm. Hort. (New Zealand) Dec. 1987:28–29.

Anon. 2003. Schede pomologiche. Kiwi. *Actinidia deliciosa*. Green Light®. Inf. Agr. 59(39):73–74.

Atkinson, R. G., G. Cipriani, D. J. Whittaker, and R. C. Gardner. 1997. The allopolyploid origin of kiwifruit, *Actinidia deliciosa* (Actinidiaceae). Pl. Syst. Evol. 205:111–124.

Bank, R., and R. Ferguson. 1986. Almost ten times as much vitamin C. New Zealand Kiwifruit Dec. 1986:23.

Baranec, T., and A. Murín. 2003. Karyological analyses of some Korean woody plants. Biologia 58:797–804.

Batchelor, J., and K. Miyabe. 1893. Ainu economic plants. Trans. Asiatic Soc. Japan 21:198–240.

Beatson, R. A. 1992. Inheritance of fruit characters in *Actinidia deliciosa*. Acta Hort. 297:79–86.

Belrose, Inc. 2005. World kiwifruit review. 2005 ed. Belrose, Inc., Pullman, WA.

Ben-Arie, R., J. Gross, and L. Sonego. 1982. Changes in ripening-parameters and pigments of the Chinese gooseberry (kiwi) during ripening and storage. Scientia Hort. 18:65–70.

Berestova, G. N. 1970. Wild forms of *Actinidia* and Chinese magnolia vine in the Primorye Territory. Tr. Prikl. Bot. Genet. Sel. 42:298–304.

Bergamini, A. 1991. "Top Star"®: il nuova kiwi a frutto liscio. Inf. Agr. 47(30):43–45.

Blanchet, P. 1995. Nouvelle variété de kiwi précoce MontCap®. Arb. Fruit. 486:17–19.

Blanchet, P., S. Brown, A.-M. Hirsch, D. Marie, and K. Watanabe. 1992. Détermination des niveaux de ploïdie dans le genre *Actinidia* Lindl. par cytométrie en flux. Fruits 47:451–460.

Blanchet, P., and J. Chartier. 1991. Genetic variability among the progeny of 'Hayward' kiwifruit. Acta Hort. 297:87–92.

Blanchet, P., and J. Chartier. 1998. Sélection de kiwis chinois pour les zones chaudes ChinaBelle® et PolliChina®. Arb. Fruit. 513:37–40.

Blanchet, P., J. Chartier, and P. Jacqueson. 1999. Chinabelle® un kiwi à chair jaune dans le Sud-Ouest. Arb. Fruit. 533:23–26.

Boase, M. R., and M. E. Hopping. 1995. DNA dodecaploid plants detected among somaclones of *Actinidia deliciosa* var. *deliciosa* cv. Hayward. Plant Cell Rep. 14: 319–323.

Bolle, C. 1880. Die Aktinidien-Schlinge *Actinidia polygama*, Sieb. et Zucc., ein interessantes japanisches Rankgewächs. Deutsch. Garten 1:47–52.

Bowden, W. M. 1945. A list of chromosome numbers in higher plants. I. Acanthaceae to Myrtaceae. Am. J. Bot. 32:81–92.

Boyes, S., P. Strübi, and H. Marsh. 1997. Actinidin levels in fruit of *Actinidia* species and some *Actinidia arguta* roostock-scion combinations. Lebensm.-Wiss. Technol. 30: 379–389.

Bretschneider, E. 1893. Botanicon sinicum. Notes on Chinese botany, from native and western sources. Pt II. J. China Branch Roy. Asiatic Soc. 25:1–468.

Bretschneider, E. 1898. History of European botanical discoveries in China. London, Sampson Low, Marston & Co.

Brundell, D. J. 1975. Flower development of the Chinese gooseberry (*Actinidia chinensis* Planch.). II. Development of the flower bud. New Zealand J. Bot. 13:485–496.

Bublin, M., A. Mari, C. Ebner, A. Knulst, O. Scheiner, K. Hoffmann-Sommergruber, H. Breiteneder, and C. Radauer. 2004. IgE sensitisation profiles towards green and gold kiwifruits differ among patients allergic to kiwifruit from 3 European countries. J. Allergy Clin. Immunol. 114:1169–1175.

Cano, M. P. 1991. HPLC separation of chlorophyll and carotenoid pigments of four kiwi fruit cultivars. J. Agr. Food Chem. 39:1786–1791.

Carrière, E.-A. 1872. *Actinidia kolomikta*. Rev. Hort. 1872:395–396.

Carrière, E.-A. 1874. *Actinidia volubilis*. Rev. Hort. 1874:394–396.

Chalak, L., and J. M. Legave. 1996. Oryzalin combined with adventitious regeneration for an efficient chromosome doubling of trihaploid kiwifruit. Plant Cell Rep. 16: 97–100.

Chalak, L., and J. M. Legave. 1997. Effects of pollination by irradiated pollen in Hayward kiwifruit and spontaneous doubling of induced parthenogenetic trihaploids. Scientia Hort. 68:83–93.

Chang, C-Y., and P.-S. Liu. 1984. A new species of the genus *Actinidia* from Sichuan. Bul. Bot. Res. 4:147–149.

Chang, L.-Y., Z.-X. Feng, G.-F. Fu, H.-Y. Yang, H.-M. Li, and Y. Jia. 1995. Investigations and study of fruit germplasm resource in Shanxi Province. Acta Hort. 403:30–38.

Ch'ang, T. S. 1982. Kiwifruit: the Chinese way. New Zealand J. Agr. 144(4):18–19.

Chat, J., L. Chalak, and R. J. Petit. 1999. Strict paternal inheritance of chloroplast DNA and maternal inheritance of mitochondrial DNA in intraspecific crosses of kiwifruit. Theor. Appl. Genet. 99:314–322.

Chat, J., P. Y. Dumoulin, Y. Bastard, and R. Monet. 1996. Cytometric and morphometric identification of diploid, tetraploid and pentaploid plants derived from *Actinidia arguta* ($2n = 4x$) crossed with *A. deliciosa* ($2n = 6x$). Plant Breed. 115:378–384.

Chat, J., B. Jáuregui, R. J. Petit, and S. Nadot. 2004. Reticulate evolution in kiwifruit (*Actinidia*, Actinidiaceae) identified by comparing their maternal and paternal phylogenies. Am. J. Bot. 91:736–747.

Chen, S.-D. 2003. Germplasm resources and high quality varieties of *Actinidia chinensis* Planch. in China. Acta Hort. 626:451–455.

Chen, Q.-C., S.-M. Wang, X.-W. Wu, and R.-H. Huang. 1987. A study on the main nutritional composition of the fruits of *Actinidia chinensis* var. *chinensis*. J. Wuhan Bot. Res. 5:391–396.

Cheng, C.-H., A. G. Seal, H. L. Boldingh, K. B. Marsh, E. A. MacRae, S. J. Murphy, and A. R. Ferguson. 2005. Inheritance of taste characters and fruit size and number in a diploid *Actinidia chinensis* (kiwifruit) population. Euphytica 138:185–195.

Chesoniene, L., R. Daubaras, and P. Viskelis. 2004. Biochemical composition of berries of some kolomikta kiwi (*Actinidia kolomikta*) cultivars and detection of harvest maturity. Acta Hort. 663:305–308.

Chun, W.-Y., C.-C. Chang, and F.-H. Chen. 1964. Flora Hainanica. Vol. 1. Science Press, Beijing.

Cipriani, G., R. Di Bella, and R. Testolin. 1997. Typing kiwifruit cultivars by means of RAPD markers. Acta Hort. 444:103–108.

Cipriani, G., A. Fiori, M. Moroldo, P. De Pauli, R. Messina, and R. Testolin. 2003. Screening chloroplast, mitochondrial, and nuclear DNA sequences suitable for taxonomic studies in Actinidiaceae. Acta Hort. 610:337–342.

Cipriani G., R. Testolin, and R. Gardner. 1998. Restriction-site variation of PCR-amplified chloroplast DNA regions and its implication for the evolution and taxonomy of *Actinidia*. Theor. Appl. Genet. 96:389–396.

Cipriani, G., R. Testolin, and M. Morgante. 1995. Paternal inheritance of plastids in interspecific hybrids of the genus *Actinidia* revealed by PCR-amplification of chloroplast DNA fragments. Mol. Gen. Genet. 247:693–697.

Coimbra, S., L. Torrão, and I. Abreu. 2004. Programmed cell death induces male sterility in *Actinidia deliciosa* female flowers. Plant Physiol. Biochem. 42:537–541.

Condon, J. M. 1991. Aspects of comparative vegetative morphology as an aid to *Actinidia* taxonomy. Ph.D. thesis, Univ. Canterbury, New Zealand.

Consorzio kiwigold. 2002. Jin Tao. Riv. Frutticolt. Ortofloricolt. 64(9):8.

Cossio, F., and Telch, A. 1989. L'*Actinidia arguta*: aspetti colturali, problemi e prospettive. Riv. Frutticolt. Ortofloricolt. 51(7):31–41.

Cotter, R. L., E. A. MacRae, A. R. Ferguson, K. L. McMath, and C. J. Brennan. 1991. Comparison of the ripening, storage and sensory qualities of seven cultivars of kiwifruit. J. Hort. Sci. 66:291–300.

Crowhurst, R. N., and R. C. Gardner. 1991. A genome-specific repeat sequence from kiwifruit (*Actinidia deliciosa* var. *deliciosa*). Theor. Appl. Genet. 81:71–78.

Crowhurst, R. N., R. Lints, R. G. Atkinson, and R. C. Gardner. 1990. Restriction fragment length polymorphisms in the genus *Actinidia* (Actinidiaceae). Plant Syst. Evol. 172:193–203.

Cui, Z.-X. 1981. Cultivation of *mihoutao* in China. p. 95–104. In: Qu Z.-Z. (ed.), Mihoutao de zaipei he liyong. Nongye Chubanshe, Beijing.

Cui, Z.-X. 1980. *Actinidia* research reports 1979–1980. Fruit Research Institute, Chinese Academy of Agricultural Sciences.

Cui, Z.-X. 1993. *Actinidia* in China. Shandong Scientific Press, Jinan, Shandong.

Cui, Z.-X., H.-W. Huang, and X.-G. Xiao. 2002. *Actinidia* in China. China. Agricultural Science and Technology Press, Beijing.

Cui, Z.-X., and X.-S. Huang. 1982. *Actinidia* research reports 1981–1982. Fruit Research Institute, Chinese Academy of Agricultural Sciences.

Cui, Z.-X., X.-S. Sun, H. Li, H.-W. Fan, X.-S. Huang, G.-H. Yang, Y. Zhang, and Z.-G. Yang. 1990. Germplasm resources of *Actinidia* in Yunnan Province, China. J. Crop Germplasm Resources 9(3):1–3.

Dai, Z, J. Li, R. Li, and C. Lei. 2002. Seventeen species of wild rare *Actinidia* germplasm resources in subtropical area of Guizhou province. Chinese J. Trop. Agr. 22(1):23–26, 52.

Darrow, G. M., and G. E. Yerkes. 1937. Some unusual opportunities in plant breeding. United States Department of Agriculture, Yearbook of Agriculture 1937:545–558.

de Wet, J. M. J. 1980. Origins of polyploids. p. 3–15. In: W. H. Lewis (ed.), Polyploidy: biological relevance. Plenum Press, New York.

Deng, D.-S. 2002. The eco-geographic distribution of *Actinidia kolomikta* (Maxim. & Rupr.) Maxim. and its phytogeographic significances. Bul. Bot. Res. 22:163–167.

Deng, D.-S., and T.-L. Ming. 2003. A revision of *Actinidia kolomikta*. Acta Bot. Yunn. 25: 41–45.

Deng, X.-X., and H.-M. Sen. 1986. Studies on the chromosome numbers of *Actinidia*. Acta Hort. Sin. 13:80, back cover.

Doležel, J., and J. Bartoš. 2005. Plant DNA flow cytometry and estimation of nuclear genome size. Ann. Bot. 95:99–110.

Dunn, S. T. 1911. A revision of the genus *Actinidia*, Lindl. J. Linn. Soc. London, Bot. 39:390–410.

Earp, R. 1988. The kiwifruit adventure. Dunmore Press, Palmerston North.

Earp, R. W. 1990. Export and marketing of New Zealand kiwifruit. p. 485–510 + 3 plates. In: I. J. Warrington and G. C. Weston (eds.), Kiwifruit: science and management. Ray Richards Publ. and New Zealand Soc. Hort. Sci., Auckland.

Ellacombe, H. N. 1879. *Actinidia kolomikta*. The Garden 15(397):516.

Esti, M., M. C. Messia, P. Bertocchi, F. Sinesio, E. Moneta, A. Nicotra, P. Fantechi, and G. Palleschi. 1998. Chemical compounds and sensory assessment of kiwifruit (*Actinidia chinensis* (Planch.) var. *chinensis*): electrochemical and multivariate analyses. Food Chem. 61:293–300.

Evreinoff, V. A. 1934. *Actinidia arguta* Planch. Nouvel arbuste fruitier. Rev. Hort. 106(1): 69–70.

Evreinoff, V. A. 1949. Notes sur les variétés d'*Actinidia*. Rev. Hort. 121:155–158.

Fairchild, D. 1913. Some Asiatic *Actinidia*s. p. 7–12 + 2 plates. In: Circular 110 (Miscellaneous Papers), Bureau of Plant Industry, United States Department of Agriculture. Government Printing Office, Washington, DC.

Fairchild, D. 1927. The fascination of making a plant hybrid; being a detailed account of the hybridization of *Actinidia arguta* and *Actinidia chinensis*. J. Hered. 18:49–62.

FAO (Food and Agricultural Organization) 1996. Russia: country report to the FAO International Technical Conference on plant genetic resources, Leipzig, 1996. www.fao.org/ag/Agp/AGPS/Pgrfa/pdf/urss.pdf

Ferguson, A. R. 1983. E. H. Wilson, Yichang, and the kiwifruit. Arnoldia 43(4):24–35.

Ferguson, A. R. 1984. Kiwifruit: a botanical review. Hort. Rev. 6:1–64.

Ferguson A. R. 1990a. The genus *Actinidia*. p. 15–35 + 5 plates. In: I. J. Warrington and G. C. Weston (eds.), Kiwifruit: science and management. Ray Richards Publ. and New Zealand Soc. Hort. Sci., Auckland.

Ferguson A. R. 1990b. Botanical nomenclature: *Actinidia chinensis*, *Actinidia deliciosa*, and *Actinidia setosa*. p. 36–57 + 2 plates. In: I. J. Warrington and G. C. Weston (eds.), Kiwifruit: science and management. Ray Richards Publ. and New Zealand Soc. Hort. Sci., Auckland.

Ferguson A. R. 1990c. The kiwifruit in China. p. 155–164 + 3 plates. In: I. J. Warrington and G. C. Weston (eds.), Kiwifruit: science and management. Ray Richards Publ. and New Zealand Soc. Hort. Sci., Auckland.

Ferguson, A. R. 1990d. Kiwifruit (*Actinidia*). Acta Hort. 290:603–653.

Ferguson, A. R. 1997. Kiwifruit (Chinese gooseberry). p. 319–323. In: The Brooks and Olmo register of fruit & nut varieties. 3rd Ed. ASHS Press, Alexandria, VA.

Ferguson, A. R. 1999a. Kiwifruit cultivars: breeding and selection. Acta Hort. 498:43–51, 194, 195.

Ferguson, A. R. 1999b. New temperate fruits: *Actinidia chinensis* and *Actinidia deliciosa*. p. 342–347. In: J. Janick (ed.), Perspectives in new crops and new uses. ASHS Press, Alexandria, VA.

Ferguson, A. R. 2003. Le cultivar di actinidia, 2003—una prospettiva dalla Nuova Zelanda. p. 51–67. In: G. Costa (ed.), Actinidia, la novità frutticolo del XX secolo. Convegno Nazionale del Società Orticolo Italiana, 21 November 2003. Camera di Commercio Industria Artigianato e Agricoltura di Verona, Verona.

Ferguson, A. R. 2004. 1904—the year that kiwifruit (*Actinidia deliciosa*) came to New Zealand. New Zealand J. Crop. Hort. Sci. 32:3–27.

Ferguson, A. R., and E. G . Bollard. 1990. Domestication of the kiwifruit. p. 165–246 + 3 plates. In: I. J. Warrington and G. C. Weston (eds.), Kiwifruit: science and management. Ray Richards Publ. and New Zealand Soc. Hort. Sci., Auckland.

Ferguson, A. R., and R. M. Davision. 1986. *Actinidia deliciosa*. p. 1–14. In: A. H. Halevy (ed.), CRC handbook of flowering, vol. 5. CRC Press, Boca Raton, FL.

Ferguson, A. R., and L. R. Ferguson. 2003. Are kiwifruit really good for you? Acta Hort. 610:131–138.

Ferguson, [A.]R., R. Lowe, M. McNeilage, and H. Marsh. 1999. “Hort16A”: un nuova kiwi a polpa gialla dalla Nuova Zelanda. Riv. Frutticolt. Ortofloricolt. 61(12):24–29.

Ferguson, A. R., and E. A. MacRae. 1991. Vitamin C in *Actinidia*. Acta Hort. 297:481–487.

Ferguson, A. R., I. E. W. O’Brien, and G.-J. Yan. 1997. Ploidy in *Actinidia*. Acta Hort. 444:67–71.

Ferguson, A. R., A. G. Seal, M. A. McNeilage, L. G. Fraser, C. F. Harvey, and R. A. Beatson. 1996. Kiwifruit. p. 371–417. In: J. Janick and J. N. Moore (eds.), Fruit breeding, Vol. 2, Vine and small fruits. Wiley, New York.

Ferguson, A. R., and R. Stanley. 2003. Kiwifruit. p. 3425–3431. In: B. Caballero, L. Trugo, and P. Finglas (eds.), Encyclopedia of food sciences and nutrition, 2nd ed., Academic Press, London.

Finet, A., and F. Gagnepain. 1907. Dilléniacées. p. 12–28. In: F. Gagnepain (ed.), Flore générale de l’Indo-Chine. Masson et Cie, Paris.

Finn, C. 1999. Temperate berry crops. p. 324–334. In: J. Janick (ed.), Perspectives on new crops and new uses. Alexandra, ASHS Press, Alexandra, VA.

Franchet, A. 1882. Les plantes du Père Incarville dans l’herbier du Muséum d’Histoire Naturelle de Paris. Bul. Soc. Bot. France 29:2–14.

Frankel, O. H., and E. Bennett. 1970. Genetic resources in plants—their exploration and conservation. Blackwell Sci. Publ., Oxford.

Fraser, L. G., and C. F. Harvey. 1986. Somatic embryogenesis from anther-derived callus in two *Actinidia* species. Scientia Hort. 29:335–346.

Fraser, L. G., C. F. Harvey, and J. Kent. 1992. Ploidy manipulations of kiwifruit in tissue culture. Acta Hort. 297:109–114.

Fuke, Y., K. Sasago, and H. Matsuoka. 1985. Determination of chlorophylls in kiwi fruit and their changes during ripening. J. Food Sci. 50:1220–1223.

Gan, C.-F. 1983. A new form of *Actinidia eriantha* Benth. Guihaia 3:18.

Gao, X.-Z., and M. Xie. 1990. A survey of recent studies on *Actinidia* species in China. Acta Hort. 282:43–52.

Georgeson, C. C. 1891. The economic plants of Japan. III. Fruit bearing vines. Am. Garden. 12(3):136–143, 147.

Gilbert, J. M., H. Young, R. D. Ball, and S. M. Murray. 1996. Volatile flavor compounds affecting consumer acceptability of kiwifruit. J. Sensory Studies 11:247–259.

Gilg, E .1893. Dilleniaceae. p. 100–128. In: H.[G. A.] Engler and K.[A. E.] Prantl (eds.), Die naturlichen Pflanzenfamilien. Teil 3, Abt. 6, Lief 80. Verlag Wilhelm Engelmann, Lepzig.

Goldblatt, P. 1980. Polyploidy in angiosperms: monocotyledons. p. 219–239. In: W. H. Lewis (ed.), Polyploidy: biological relevance. Plenum Press, New York.

Gotsik, Ya. K. 1955. Growing of some far-eastern lianes in the Botanical Garden of the Academy of Sciences of the Ukranian SSR. Trudy Bot. Sada Akad. Ukrain. 3:38–44.

Graebener, [L.] 1894. Eine neue Beerenobstpflanze. Gartenflora 43:78–79.

Graebener, L. 1895. Eine Schlingpflanze mit essbaren Früchten. Gartenflora 44:534–535.

Grant, V. 1963. The origin of adaptations. Columbia Univ. Press, New York.

Greilhuber, J., J. Doležel, M. A. Lysák, and M. D. Bennett. 2005. The origin, evolution and proposed stabilization of the terms 'genome size' and 'C-value' to describe nuclear DNA contents. Ann. Bot. 95:255–260.

Gui, Y.-L. 1981. A comparative morphological observations of *Actinidia chinensis* Planch. var. *chinensis* and *A. chinensis* Planch. var. *hispida*. Acta Phytotaxon. Sin. 19:304–307 + plate.

Gui, Y., S. Hong, S. Ke, and R. M. Skirvin. 1993. Fruit and vegetative characteristics of endosperm-derived kiwifruit (*Actinidia chinensis* F) plants. Euphytica 71:57–62.

Hallett, I. C., and P. W. Sutherland. 2005. Structure and development of kiwifruit skins. Int. J. Plant Sci. 166:693–704.

Hallett, I. C., T. F. Wegrzyn, and E. A. MacRae. 1995. Starch degradation in kiwifruit: in vivo and in vitro ultrastructural studies. Int. J. Plant Sci. 156:471–480.

Han, T., L.-P. Li, and H.-Y. Zhang. 2003. Progress of research on postharvest physiology of kiwifruit in China. Acta Hort. 610:307–315.

Hao, R. 1982. Germplasm resources of wild fruits in the Chang Bai Shan mountain region. Acta Hort. Sin. 9:9–16.

Hara, H. 1966. The flora of eastern Himalaya. Univ. Tokyo Press, Tokyo.

Harlan, J. R. 1970. Evolution of cultivated plants. p. 19–32. In: O. H. Frankel and E. Bennett (eds.), Genetic resources in plants—their exploration and conservation. Blackwell Sci. Pub., Oxford.

Harvey, C. F., L. G. Fraser, and G. P. Gill. 1997. Sex determination in *Actinidia*. Acta Hort. 444:85–88.

Harvey, C. F., L. G. Fraser, and J. Kent. 1992. *Actinidia* seed development in interspecific crosses. Acta Hort. 297:71–78.

Harvey, C. F., G. P. Gill, L. G. Fraser, and M. A. McNeilage. 1997. Sex determination in *Actinidia*. 1. Sex-linked markers and progeny sex ratio in diploid *A. chinensis*. Sex. Plant Reprod. 10:149–154.

Hassall, A. K., G. J. Pringle, and E. A. MacRae. 1998. Development, maturation and postharvest responses of *Actinidia arguta* (Sieb. et Zucc.) Planch. ex Miq. fruit. New Zealand J. Crop Hort. Sci. 26:95–108.

He, Z.-C., H.-W. Huang, and Z. Yang. 2003. Cytogenetic study of diploid *Actinidia chinensis*—karyotype, morphology of sex chromosomes at primary differentiation stage and evolutionary significance. Acta Hort. 610:379–385.

He, Z.-C., J.-Q. Li, Q. Cai, and Q. Wang. 2005. The cytology of *Actinidia*, *Saurauia* and *Clematoclethra* (Actinidiaceae). Bot. J. Linn. Soc. 147:369–374.

He, Z.-C., S.-M. Wang, H. Huang, and H.-Q. Huang. 1998. Study on chromosome numbers of 6 species and 1 variety in *Actinidia* Lindl. J. Wuhan Bot. Res. 16:299–301.

He, Z.-C., X.-Y. Zhang, Y. Zhong, and L. Ye. 2000a. Phylogenetic relationships of *Actinidia* and related genera based on micromorphological characters of foliar trichomes. Genet. Res. Crop Evol. 47:627–639.

He, Z.-C., Y. Zhong, H.-T. Liu, X.-H. Tang , L. Ye, D.-S. Huang, and L.-M. Xu . 2000b. Quantitative taxonomic analyses of *Actinidia* (Actinidiaceae) in China based on micromorphological characters of foliar trichomes. Acta Phytotaxon. Sin. 38:121–136.

Henry, A. 1893. Notes on economic botany of China. Presbyterian Mission Press, Shanghai. 2nd facs. ed. 1986, Boethius Press, Kilkenny, Ireland.

Hirsch, A. M., D. Fortune, and P. Blanchet. 1990. Study of dioecism in kiwifruit, *Actinidia deliciosa*, Chevalier. Acta Hort. 282:367–376.

Hirsch, A.-M., A. Longeon, and M. Guyot. 2002. Fraxin and esculin: two coumarins specific to *Actinidia chinensis* and *A. deliciosa* (kiwifruit). Biochem. Syst. Ecol. 30:55–60.

Hirsch, A.-M., R. Testolin, S. Brown, J. Chat, D. Fortune, J. M. Bureau, and D. de Nay. 2001. Embryo rescue from interspecific crosses in the genus *Actinidia* (kiwifruit). Plant. Cell Rep. 20:508–516.

Ho, P. H. and N. V. Duong. 1960. Cay-co mien nam Viet-nam [Flora of South Vietnam]. Ministry of National Education, Saigon.

Hooker, J. D. 1896. *Actinidia polygama*. Curtis's Botanical Mag. 122:Tab. 7497.

Hopping, M. E. 1993. Preparation and preservation of nuclei from plant tissues for quantitative DNA analysis by flow cytometry. New Zealand J. Bot. 31:391–401.

Hopping, M. E. 1994a. Flow cytometric analysis of *Actinidia* species. New Zealand J. Bot. 32:85–93.

Hopping, M. E. 1994b. Seasonal changes in fluorescence intensity of kiwifruit nuclei stained with propidium iodide and measured by flow cytometry. New Zealand J. Bot. 32:237–245.

Horikawa, Y. 1972. Atlas of the Japanese flora: an introduction to plant sociology of East Asia. Gakken, Tokyo.

Horikawa, Y. 1976. Atlas of the Japanese flora II: an introduction to plant sociology of East Asia. Gakken, Tokyo.

Hu, Z.-R., Y. Yuan, and S.-W. Yi. 2003. Germplasm resources and main distribution of wild Chinese gooseberry in Yunnan Province. p. 275–279. In: H.-W. Huang (ed.), Advances in *Actinidia* research (II). Science Press, Beijing.

Huang, H.-W., 1999. Nuove varietà di *Actinidia deliciosa* e *A. chinensis* ottenute in Cina. Riv. Frutticolt. Ortofloricolt. 61(12):18–22.

Huang, H.-W., F. Dane, Z.-Z. Wang, Z.-W. Jiang, R.-H. Huang, and S.-M. Wang. 1997. Isozyme inheritance and variation in *Actinidia*. Heredity 78:328–336.

Huang, H.-W., and A. R. Ferguson. 2001. Kiwifruit in China. New Zealand J. Crop Hort. Sci. 29:1–14.

Huang, H.-W., and A. R. Ferguson. 2003. Kiwifruit (*Actinidia chinensis* and *A. deliciosa*) plantings and production in China, 2002. New Zealand J. Crop Hort. Sci. 31:197–202.

Huang, H.-W., J.-J. Gong, S.-M. Wang, Z.-C. He, Z.-H. Zhang, and J.-Q. Li. 2000a. Genetic diversity in the genus *Actinidia*. Chinese Biodiversity 8:1–12.

Huang, H.-W, J.-J. Gong, S.-M. Wang, Z.-C. He, Z.-H. Zhang, J.-Q. Li, and Z.-W. Jiang. 2000b. Genetic diversity in genus *Actinidia*. p. 65–79. In: H.-W. Huang (ed.), Advances in *Actinidia* research. Science Press, Beijing.

Huang, H.-W., J. Li, P. Lang, and S. Wang. 1999. Systematic relationships in *Actinidia* as revealed by cluster analysis of digitized morphological descriptors. Acta Hort. 498:71–78.

Huang, H.-W., Z.-Z. Li, J.-Q. Li, T. L. Kubisiak, and D. R. Layne. 2002a. Phylogenetic relationships in *Actinidia* as revealed by RAPD analysis. J. Am. Soc. Hort. Sci. 127:759–766.

Huang, H.-W., S.-M. Wang, R.-H. Huang, Z.-W. Jiang, and Z.-H. Zhang. 2002b. 'Jintao', a novel, hairless, yellow-fleshed kiwifruit. HortScience 37:1135–1136.

Huang, H.-W., S. Wang, Z. Jiang, Z. Zhang, and J. Gong. 2003. Exploration of *Actinidia* genetic resources and development of kiwifruit industry in China. Acta Hort. 610:29–43.

Huang, H.-W., Y. Wang, Z.-H. Zhang, Z.-W. Jiang, and S.-M. Wang. 2004. *Actinidia* germplasm resources and kiwifruit industry in China. HortScience 39:1165–1172.

Huang, R.-H., and S.-M. Wang. 1995. *Actinidia persicina*—a new species of *Actinidia*. J. Wuhan Bot. Res. 13:113–115.

Huang, W.-G., G. Cipriani, M. Morgante, and R. Testolin. 1998. Microsatellite DNA in *Actinidia chinensis*: isolation, characterisation, and homology in related species. Theor. Appl. Genet. 97:1269–1278.

Huang, Z.-F., M.-Y. Liang, C.-G. Huang, and R.-G. Li. 1983. A preliminary study on the character and nutritive composition of *Actinidia* fruits. Guihaia 3:53–56, 66.

Ito, K., and H. Kaku. 1883. Figures and descriptions of plants in Koshikawa Botanical Garden. (Translated by J. Matsumura.) Vol. 2. Z.P. Maruya, Tokyo.

Jaeger, S. R., and F. R. Harker. 2005. Consumer evaluation of novel kiwifruit: willingness-to-pay. J. Sci. Food Agr. 85:2519–2526.

Jaeger, S. R., K. L. Rossiter, W. V. Wismer, and F. R. Harker. 2003. Consumer-driven product development in the kiwifruit industry. Food Qual. Pref. 14:187–198.

Janick, J. 1955. Inheritance of sex in tetraploid spinach. Proc. Am. Soc. Hort. Sci. 66: 361–363.

Janick, J., and E. C. Stevenson. 1955. The effects of polyploidy on sex expression in spinach. J. Hered. 46:151–156 + plate.

Jia, B., L.-W. Zhu, X. Yu, L.-J. Lu, and Y.-F. Wang. 2005. RAPD analyses on germplasm resources in genus *Actinidia*. J. Anhui Agr. Univ. 32:381–384.

Jiang, H.-Z. 1995. Two new species of *Actinidia* from Yunnan, China. J. Southwest Agr. Univ. 17:93–96.

Jordán, M. J., C. A. Margaría, P. E. Shaw, and K. L Goodner. 2002. Aroma active components in aqueous kiwi fruit essence and kiwi fruit puree by GC-MS and multidimensional GC/GC-O. J. Agr. Food Chem. 50:5386–5390.

Jung, Y.-H., K.-H. Kim, S.-H. Kang, S.-J. Jun, M.-Y. Oh, and S.-C. Kim. 2003a. Phylogenetic analysis of the genus *Actinidia* in Korea inferred from two non-coding chloroplast DNA sequences. Korean J. Genet. 25:95–101.

Jung, Y.-H., S.-C. Kim, M. Kim, K.-H. Kim, H.-M. Kwon, and M.-Y. Oh. 2003b. Chloroplast inheritance patterns in *Actinidia* hybrids determined by single stranded conformation polymorphism analysis. Mol. Cells 15:277–282.

Kabaluk, J. T., C. Kempler, and P. M. A. Toivonen. 1997. *Actinidia arguta*—characteristics relevant to commercial production. Fruit Var. J. 51:117–122.

Kamota, F., H. Honjo, and M. S. Kim. 1989. Estimation of favourable locations for kiwifruit (*Actinidia deliciosa* Liang et Ferguson) cultivation in Japan. Bul. Fruit Tree Res. Sta. 16:99–113.

Kawagoe, T., and N. Suzuki. 2004. Cryptic dioecy in *Actinidia polygama*: a test of the pollinator attraction hypothesis. Can. J. Bot. 82:214–218.

Ke, S.-Q., R.-H. Huang, S.-M. Wang, Z.-T. Xiong, and Z.-W. Wu. 1992. Studies on interspecific hybrids of *Actinidia*. Acta Hort. 297:133–139.

Keng, H. 1972. Actinidiaceae. p. 139–141. In T. Smitinand and K. Larsen (eds.), Flora of Thailand. Vol. 2, Pt 2. Applied Scientific Research Corporation of Thailand, Bangkok.

Kim, S.-C., Y.-H. Jung, M. Kim, C.-H. Kim, S.-C. Koh, and S.-H. Kang. 2003. Genetic relationships of genus *Actinidia* based on random amplified polymorphic DNA analysis. J. Korean Soc. Hort. Sci. 44:340–344.

Kokudo, K., K. Beppu, I. Kataoka, T. Fukuda, S. Mabuchi, and K. Suezawa. 2003. Phylogenetic classification of introduced and indigenous *Actinidia* in Japan and identification of interspecific hybrids using RAPD analysis. Acta Hort. 610:351–356.

Kolbasina, E. I. 1963. A contribution to the ecology of wild *Actinidia kolomikta* on Sakhalin Island. Tr. Sakhalin. Kompleksn. Nauchno-Issled. Inst. Akad. Nauk SSSR Sib. Odt. 13:71–78.

Kolbasina, E. I. 1969. On the distribution of *Actinidia* in Sakhalin and the Kuril Islands. Bot. Zh. (Leningrad) 54:1583–1585.

Kolbasina, E. I. 1970. Distribution and diversity of forms of *Actinidia arguta* in the islands of Sakhalin and Kunashir. Rastitelnye Resursy 6:212–216.

Lauche, W. 1879. *Actinidia polygama* Sieb. Monats. Ver. Beford. Gartenb. K. Preuss. Staat. Gesellsch. Gartenfr. Berlins 22: 319–321 + Plate 4.

Lavallée, A. 1885. Arboretum Segrezianum. Icones selectæ arborum et fruticum in Hortis Segrezianis collectorum. Librarie J.-B. Ballière et Fils, Paris.

Lee, B.-S., M.-H. Lee, S.-I. Hwang, S.-C. Kim, S.-S. Han, and U. Lee. 2004. Characteristics of F1 seeds of the cross between *Actinidia arguta* and *A. deliciosa*. Korean J. Breed. 36:345–349.

Lee, S.-H. 1990. Kiwi fruit resources and production in China. Acta Hort. 282:57–63.

Leichtlin, M. 1895. Eigenschaften der *Actinidia polygama* als Fruchtpflanze. Möller's Deu. Gärt.-Zeit. 10:98.

Li, H.-L. 1943. Notes on the flora of Indo-China. J. Arnold Arb. 24:362–374.

Li, H.-.L. 1952. A taxonomic review of the genus *Actinidia*. J. Arnold Arb. 33:1–61.

Li, H.-L. 1976. *Actinidia*. p. 585–591. In: H.-L. Li, T.-S. Liu, T.-C. Huang, T. Koyama, C. E. DeVol (eds.), Flora of Taiwan, Vol. 2 Angiospermae. Epoch Publ. Co., Taipei.

Li, J.-Q., Q. Cai, and H.-W. Huang. 2000. On the phylogeny of the genus *Actinidia* Lindley. p. 80–86. In: H.-W. Huang. (ed.), Advances in *Actinidia* research. Science Press, Beijing.

Li, J.-Q., H.-W. Huang, and T. Sang. 2002a. Molecular phylogeny and infrageneric classification of *Actinidia* (Actinidiaceae). Syst. Bot. 27:408–415.

Li, J.-Q., X.-W. Li, and D. D. Soejarto. 2006. Actinidiaceae. Draft for: The flora of China, Vol. 12. http://flora.huh.Harvard.edu/china/mss/volume12/Actinidiaceae-AGH_reviewing.htm.

Li, R.-G., C.-G. Huang, M.-Y. Liang, and Z.-F. Huang. 1985. Investigation of germplasm resources of *Actinidia* in Guangxi. Guihaia 5:253–267.

Li, R.-G., J.-W. Li, X.-.G. Wang, L. Mo, and M.-Y. Liang. 2002b. Three new varieties of *Actinidia* Lindl. from Guangxi. Guihaia 22:385–387.

Li, R.-G., J.-W. Li, X.-G. Wang, L. Mo, and M.-Y. Liang. 2003a. Nine new species of *Actinidia* Lindl. Guihaia 23:193–202.

Li, R.-G., M.-Y. Liang, J.-W. Li, and S.-H. Mao. 1996. Studies on the biological characteristics of genus *Actinidia*. Guihaia 16:265–272.

Li, R.-J., Z.-Y. Shang, and J.-Z. Zhang. 1988. A brief report on the chromosome number of *Actinidia valvata*. Shaanxi Forest Sci. Technol. 3:9.

Li, Z., H. Huang, Z. Jiang, J. Li, and T. L. Kubisiak. 2003b. Phylogenetic relationships in *Actinidia* as revealed by RAPDs and PCR-RFLPs of mtDNA. Acta Hort. 610:387–396.

Liang, C.-F. 1975. Classification of *Actinidia chinensis* Planch. Acta Phytotaxon. Sin. 13:32–35 + plate.

Liang, C.-F. 1982a. New taxa of the genus Actinidia Lindl. Guihaia 2:1–6.

Liang, C.-F. 1982b. An addition to the infraspecific taxa of *Actinidia chinensis* Planch. Acta Phytotaxon. Sin. 20:101–104.

Liang, C.-F. 1983. On the distribution of Actinidias. Guihaia 3:229–248.

Liang, C.-F. 1984 *Actinidia*. p. 196–268, 309–324. In: K.-M. Feng (ed.), Flora Reipublicae Popularis Sinicae, 49/2. Science Press, Beijing.

Liang, C.-F. 1988. New species *Actinidia guilinensis*. Guihaia 8:129–131.

Liang, C.-F. 1991. Two new varieties of *Actinidia eriantha* Benth. Guihaia 11:118 + plate.

Liang, C. F., and A. R. Ferguson. 1984. Emendation of the Latin Name of *Actinidia chinensis* Planch. var. *hispida* C. F. Liang. Guihaia 4:181–182.

Liang, C. F., and A. R. Ferguson. 1986. The botanical nomenclature of the kiwifruit and related taxa. New Zealand J. Bot. 24:183–184.

Liang, C.-F., and Y.-X. Lu. 1989. New species *Actinidia lijiangensis*. Guihaia 9:21–23.

Lin, T.-H., and X.-Y. Xiong. 1991. A new variety of *Actinidia deliciosa*. Guihaia 11:117 + plate.

Lindley, J. 1836. A natural system of botany. 2nd ed. Longman, London.

Lindsay, G. C. 1995. DNA content of nuclei of *Actinidia deliciosa* var. *deliciosa* 'Hayward' (kiwifruit) analysed by image cytometry. New Zealand J. Bot. 33:243–255.

Linsley-Noakes, G. C. 1990. Release of the locally selected kiwifruit cultivar Donné. NIVV/FFTRI INFO 589. (Fruit Fruit Technol. Res. Inst., Stellenbosch)

Lintas, C., S. Adorisio, M. Cappelloni, and F. Monastra. 1991. Composition and nutritional evaluation of kiwifruit grown in Italy. New Zealand J. Crop Hort. Sci. 19:341–344.

Lu, L.-X., M.-C. Tao, and Y.-X. Pan. 1984. Observation on the chromosome and meioses of pollen mother cells in "Maohua-Gooseberry" (*Actinidia eriantha* Benth.). Fujian Nongxueyuan Xuebao (J. Fujian Agr. Col.) 15:25–30.

Lucas, J. S. A., S. A. Lewis, and J. O'B. Hourihane. 2003. Kiwi fruit allergy: a review. Ped. Allergy Immunol. 14:420–428.

McGhie, T. K., and G. D. Ainge. 2002. Color in fruit of the genus *Actinidia*: carotenoid and chlorophyll compositions. J. Agr. Food Chem. 50:117–121.

McNeilage, M. A. 1988. Cytogenetics, dioecism and quantitative variation in *Actinidia*. Ph.D. thesis, Univ. Auckland, New Zealand.

McNeilage, M. A. 1991a. Gender variation in *Actinidia deliciosa*, the kiwifruit. Sex. Plant Reprod. 4:267–273.

McNeilage, M. A. 1991b. Sex expression in fruiting male vines of kiwifruit. Sex. Plant Reprod. 4:274–278.

McNeilage, M. A. 1997. Progress in breeding hermaphrodite kiwifruit cultivars and understanding the genetics of sex determination. Acta Hort. 444:73–78.

McNeilage, M. A., and J. A. Considine. 1989. Chromosome studies in some *Actinidia* taxa and implications for breeding. New Zealand J. Bot. 27:71–81.

McNeilage, M. A., and S. Steinhagen. 1998. Flower and fruit characters in a kiwifruit hermaphrodite. Euphytica 101:69–72.

Marsh, K., S. Attanayake, S. Walker, A. Gunson, H. Boldingh, and E. MacRae. 2004. Acidity and taste in kiwifruit. Postharv. Biol. Technol. 32:159–168.

Marsh, H., M. McNeilage, and I. Gordon. 1999. Breeding value of parents in kiwifruit (*Actinidia deliciosa*). Acta Hort. 498:85–92.

Marsh, K., K. Rossiter, K. Lau, S. Walker, A. Gunson, and E. MacRae. 2003. The use of fruit pulps to explore flavour in kiwifruit. Acta Hort. 610:229–237.

Martin, P. 2005. Spot the difference. New Zealand Kiwifruit J. 169:12–15.

Martin, R. A. 2003. The production and marketing of New Zealand kiwifruit. Acta Hort. 610:25–28.

Martin, R. A., and P. Luxton. 2005. The successful commercialisation of ZESPRI™ Gold Kiwifruit. Acta Hort. 694:35–40.

M[asters], M. T. 1880. *Actinidia kolomikta*. Gardeners' Chronicle Ser. 2, 24:262.

Matich, A. J., H. Young, J. M. Allen, M. Y. Wang, S. Fielder, M. A. McNeilage, and E. A. MacRae. 2003. *Actinidia arguta*: volatile compounds in fruit and flowers. Phytochemistry 63:285–301.

Matsunaga, S., A. Sakai, S. Kawano, and T. Kuroiwa. 1996. Cytological analysis of the mature pollen of *Actinidia deliciosa* (kiwifruit). Cytologia 61:337–341.

Mayr, E. 1942. Systematics and the origin of species. Columbia Univ. Press, New York.

Merrill, E. D. 1938. New or noteworthy Indo-Chinese plants. J. Arnold Arb. 19:21–70.

Messina, R. 1993. Microsporogenesis in male-fertile cv. Matua and male-sterile cv Hayward of *Actinidia deliciosa* var. *deliciosa* (kiwifruit). Advan. Hort. Sci. 7:77–81.

Messina, R., R. Testolin, and M. Morgante. 1991. Isozymes for cultivar identification in kiwifruit. HortScience 26: 899–902.

Messina R., M. Vischi, S. Marchetti, R. Testolin, and N. Milani. 1990. Observations on subdioeciousness and fertilization in a kiwifruit breeding program. Acta Hort. 282:377–386.

Meyer, F. N. 1911. Agricultural explorations in the fruit and nut orchards of China. Bul. 204, Bureau of Plant Industry, United States Department of Agriculture, Government Printing Office, Washington DC.

Meyer, R. 1987. Kiwifruit varieties for backyard gardeners in warm-winter areas. J. Calif. Rare Fruit Growers 19:45–48.

Michurin, I. V. 1949. Selected works. Foreign Languages Publishing House, Moscow.

Minchin, P. E. H., N. De Silva, W. P. Snelgar, A. C. Richardson, and T. G. Thorp. 2003. Modelling of colour development in the fruit of *Actinidia chinensis* 'Hort16A'. New Zealand J. Crop. Hort. Sci. 31:41–53.

Montefiori, M., G. Costa, T. McGhie, and R. Ferguson. 2003. I pigmenti responsabili della colorazione dei frutti in *Actinidia*. p. 99–104. In: G. Costa (ed.), Actinidia, la novità frutticolo del XX secolo. Convegno Nazionale della Società Orticolo Italiana, 21 November 2003. Verona, Camera di Commercio Industria Artigianato e Agricoltura di Verona, Italy.

Montefiori, M., G. Costa, T. McGhie, and R. Ferguson. 2004. Indagini sul colore della polpa dei frutti di alcune specie di *Actinidia*. Riv. Frutticolt. Ortofloricolt. 66(10):43–45, 47, 48.

Montefiori, M., T. K. McGhie, G. Costa, and A. R. Ferguson. 2005. Pigments in the fruit of red-fleshed kiwifruit (*Actinidia chinensis* and *A. deliciosa*). J. Agr. Food. Chem. 53:9526–9530.

Moore, J. N. 1970. Cytokinin-induced sex conversion in male clones of *Vitis* species. J. Am. Soc. Hort. Sci. 95:387–393.

Mouat, H. M. 1958. New Zealand varieties of yang-tao or Chinese gooseberry. New Zealand J. Agr. 97:161, 163, 165.

Mu, S.-K., L. G. Fraser, and C. F. Harvey. 1990. Rescue of hybrid embryos of *Actinidia* species. Scientia Hort. 44:97–106.

Mu, X.-J., D.-R. Tsai, H.-X. An, and W.-L. Wang. 1992. Embryology and embryo rescue of interspecific hybrids in *Actinidia*. Acta Hort. 297:93–98.

Muggleston, S., M. McNeilage, R. Lowe, and H. Marsh. 1998. Breeding new kiwifruit cultivars: the creation of Hort16A and Tomua. Orchardist New Zealand 71(8):38–40.

Murray, B. G. 2002. Trees, maps and FISH: the application of genome based technologies to the analysis of chromosome evolution. Curr. Genom. 3:539–550.

Nakai, T. 1933. Notulae ad plantas Japoniae & Koreae XLIII. Bot. Mag. (Tokyo) 47:235–267.

Nakajima, G. 1942. Cytological studies in some flowering dioecious plants, with special reference to the sex chromosomes. Cytologia 12:262–270.

Nath, D. M. 1960. Botanical survey of the southern Shan states. Burma Res. Soc. 50th Anniversary Publ. 1:161–418.

Nee, C., and T. Tsay. 1992. Kiwifruit in Taiwan. Acta Hort. 297:175–182.

Nei, M. 1987. Molecular evolutionary genetics. Columbia Univ. Press, New York.

Nicotra, A., L. Moser, E. Caboni, C. Damiano, A. M. Simeone, F. Monastra, C. Fideghelli, R. F. De Salvador, L. Rivalta, M. Dradi, and A. Bergamini. 1999. Breeding program at the Istituto Sperimentale per la Frutticoltura—Roma: Recent acquisitions. Acta Hort. 498:65–70.

Nishiyama, I., T. Fukuda, and T. Oota. 2004. Varietal differences in actinidin concentration and protease activity in the fruit juice of *Actinidia arguta* and *Actinidia rufa*. J. Japan. Soc. Hort. Sci. 73:157–162.

Nishiyama, I., T. Fukuda, and T. Oota. 2005. Genotypic differences in chlorophyll, lutein, and β-carotene contents in the fruits of *Actinidia* species. J. Agr. Food Chem. 53: 6403–6407.

Nishiyama, I., and T. Oota. 2002. Varietal difference in actinidin concentration and protease activity in the kiwi fruit juice. J. Japan. Soc. Food Sci. Technol. 49:401–408.

Nishiyama, I., Y. Yamashita, M. Yamanaka, A. Shimohashi, T. Fukuda, and T. Oota. 2004. Varietal differences in vitamin C content in the fruit of kiwifruit and other *Actinidia* species. J. Agr. Food Chem. 52:5472–5475.

Ohwi, J. 1965. Flora of Japan. F. G. Meyer and E. H. Walker (eds.). Smithsonian Inst., Washington, DC.

Okamoto, G., and S. Goto. 2005. Juice constituents in *Actinidia arguta* fruits produced in Shinjo, Okayama. Sci. Rep. Fac. Agr. Okayama Univ. 94:9–13.

Oliveira, M. M., and L. G. Fraser. 2005. 1.1 *Actinidia* spp. Kiwifruit. p. 2–27. In: R. E. Litz (ed.), Biotechnology of fruit and nut crops. (Biotechnology in agriculture No. 29). CABI Publ., Wallingford, UK.

Oliver, D. 1887. *Actinidia chinensis*, Planchon. Hooker's Icones Plant. 16:plate1593.

Ollitrault-Sammarcelli, F., J. M. Legave, M. Michaux-Ferriere, and A. M. Hirsch. 1994. Use of flow cytometry for rapid determination of ploidy level in the genus *Actinidia*. Scientia Hort. 57:303–313.

Orpet, E. O. 1892. *Actinidia polygama*. Garden Forest 5(228):320.

Ossani, V. 2002a. Summer 3373. Riv. Frutticolt. Ortofloricolt. 64(9):9.

Ossani, V. 2002b. Summer 4605. Riv. Frutticolt. Ortofloricolt. 64(9):10.

Pandey, K. K., L. Przywara, and P. M. Sanders. 1990. Induced parthenogenesis in kiwifruit (*Actinidia deliciosa*) induced through use of lethally irradiated pollen. Euphytica 51:1–9.

Paterson, V. J., E. A. MacRae, and H. Young. 1991. Relationships between sensory properties and chemical composition of kiwifruit (*Actinidia deliciosa*). J. Sci. Food Agr. 57:235–251.

Patterson, K., J. Burdon, and N. Lallu. 2003. 'Hort16A' kiwifruit: progress and issues with commercialisation. Acta Hort. 610:267–273.

Peng J.-J. and F.-Y. Lu. 1986 (2003). Actinidiaceae. p. 656–661. In: T.-C. Huang and Editorial Committee of the Flora of Taiwan (eds.), Flora of Taiwan, Vol. 2., 2nd ed. National Taiwan Univ., Taipei. (Database version).

Penhallow, D. P. 1884. Notes on the trees and shrubs of Northern Japan. Ann. Rep. Montreal Hort. Soc. Fruitgrowers' Assoc. Prov. Quebec 9 (1883):13–51.

Phivnil, K., K. Beppu, T. Takamura, T. Fukuda, and I. Kataoka. 2005. Flow cytometric assessment of ploidy in native resources of *Actinidia* in Japan. J. Am. Pomol. Soc. 59:44–49.

Planchon, J. E. 1847. Sur la nouvelle famille des Cochlospermées. London J. Bot. 6:294–311.

Polito, V. S., and J. A. Grant. 1984. Initiation and development of pistillate flowers in *Actinidia chinensis*. Scientia Hort. 22:365–371.

Possingham, J. V., M. Coote, and J. S. Hawker. 1980. The plastids and pigments of fresh and dried Chinese gooseberries (*Actinidia chinensis*). Ann. Bot. (London) 45:529–533.

Poyarkova, A. I. (1949) 1974. Actinidiaceae van Tiegh. p. 138–147. In: B. K. Shishkin (ed.), Malvales, Parietales, Myrtiflorae. Flora of the U.S.S.R. Vol. XV. (Translation of Flora URSS XV: 185–197.) Israel Program for Scientific Translations, Jerusalem.

Przywara, L., K. K. Pandey, and P. M. Sanders. 1988. Length of stomata as an indicator of ploidy level in *Actinidia deliciosa*. New Zealand J. Bot. 26:179–182.

Qian, Y.-Q., and D.-P. Yu. 1991. Advances in *Actinidia* research in China. Acta Hort. 297:51–55.

Qiu, B.-L. 1993. Flora of Zhejiang, Vol. 4. (ed.), Zhejiang Sci. Technol. Press, Hangzhou.

Rassam, M., and W. A. Laing. 2005. Variation in ascorbic acid and oxalate levels in the fruit of *Actinidia chinensis* tissues and genotypes. J. Agr. Food Chem. 53:2322–2326.

Rehder, A. 1896. Die Schlingpflanze *Actinidia kolomikta*. Möller's Deu. Gärt.-Zeit. 9:399–400.

Rehder, A. 1927. Manual of cultivated trees and shrubs hardy in North America. Macmillan, New York.

Richardson, A. C., K. B. Marsh, H. L. Boldingh, A. H. Pickering, S. M. Bulley, N. J. Frearson, A. R. Ferguson, S. E. Thornber, K. M. Bolitho, and E. A. MacRae. 2004. High growing temperatures reduce fruit carbohydrate and vitamin C in kiwifruit. Plant, Cell Environ. 27:423–435.

Rizet, G. 1945. Contribution à l'étude biologique et cytologique de l'*Actinidia chinensis*. C. R. Sèances Soc. Biol. Paris 139:140–142.

Rusterholz, P., and A. Husistein. 2000. Minikiwis—Aroma in Grün. Obst. Weinbau 136:289–292.

Salomon, C. 1869. Einige Notizen über verschiedene ältere und neuere Gehölze des Freilandes im botanischen Garten zu Würzburg. Gartenflora 1869:164–166.

Samadi-Maybodi, A., and M. R. Shariat. 2003. Characterization of elemental composition in kiwifruit grown in northern Iran. J. Agr. Food Chem. 51:3108–3110.

Sanada, T., and Y. Sato. 2003. Genetic resources of Asian temperate fruit. Acta Hort. 620:137–149.

Schmid, R. 1978. Reproductive anatomy of *Actinidia chinensis* (Actinidiaceae). Bot. Jahrb. Syst. Pflanzengesch. Pflanzengeogr. 100:149–195.

Schondorf. 1879. [Ueber die Actinidia kalomikta.] Monats. Ver. Beford. Gartenb. K. Preuss. Staat. Gesellsch. Gartenfr. Berlins 22:457.

Scoccianti, V., A. Speranza, R. Crinelli, G. L. Calzoni, R. Biasi, M. M. Altamura, and N. Bagni. 1999. Development-related changes of protein ubiquitination in pollen from male and female kiwifruit (*Actinidia deliciosa*). Physiol. Plant. 107:128–135.

Seager, N. 1997. Synthesis and degradation of anthocyanin in *Actinidia arguta* × *melanandra*. Acta Hort. 444:523–528.

Seager, N. G., I. J. Warrington, and E. W. Hewett. 1996. Maturation of kiwifruit grown at different temperatures in controlled environments. J. Hort. Sci. 71:639–652.

Seal, A. G. 2003. The plant breeding challenges to making kiwifruit a worldwide mainstream fresh fruit. Acta Hort. 610:75–80.

Seal, A. G., and M. A. McNeilage. 1989. Sex and kiwifruit breeding. Acta Hort. 240:35–38.

Shi, S.-D., Q.-B. Wang, and Z.-S. Zhang. 1994. New taxa of the genus *Actinidia* from Guizhou. Acta Bot. Yunn. 16:345–347.

Shim, K.-K., and Y.-M. Ha. 1999. Kiwifruit production and research in Korea. Acta Hort. 498:127–131 + plate.

Siebold, P. F. de, and J. G. Zuccarini. 1843. Plantarum quas in Japonia collegit Dr. Ph. Fr. de Siebold, genera nova, notis characteristicis delineationibusque illustrata proponunt. Abh. Math-Phys. Cl. Königl. Bayer. Akad. Wiss. 3:717–749.

Smartt, J., and N. W. Simmonds. 1995. Evolution of Crop Plants. (eds.), 2nd ed. Longman Scientific & Technical, Essex, UK.

Snelgar, W. P., A. J. Hall, A. R. Ferguson, and P. Blattmann. 2005. Temperature influences growth and maturation of fruit on 'Hayward' kiwifruit vines. Funct. Plant Biol. 32: 631–642.

Sokolovskaya, A. P., N. S. Probatova, and E. G. Rudyka. 1989. Chromosome numbers in some species of the flora of the Soviet Far East from the families Actinidiaceae, Aristolochiaceae, Fabaceae, Ranunculaceae, Saxifragaceae. Bot. Zh. 74:268–271.

Soltis, D. E., and P. S. Soltis. 1999. Polyploidy: recurrent formation and genome evolution. Trends Ecol. Evol. 14:348–352.

Soltis, D. E., P. S. Soltis, and J. A. Tate. 2003. Advances in the study of polyploidy since *Plant Speciation*. New Phytol. 161:173–191.

Sprague, T. A. 1914. *Actinidia chinensis*. Curtis's Bot. Mag. 140:Tab 8538.

Stapf, O. 1926. *Actinidia kolomikta*. Curtis's Bot. Mag. 151 ("1925"):Tab. 9093.

Start, M. A., J. Luby, R. Guthrie, and D. Filler. 1997. Abstract 073. Ploidy levels of hardy *Actinidia* accessions in the U.S. determined by flow cytometry. HortScience 32:439.

Stebbins, G. L. 1950. Variation and evolution in plants. Columbia Univ. Press, New York.

Stebbins, G. L. 1971. Chromosomal evolution in higher plants. Edward Arnold, London.

Stec, M. G. H., J. A. Hodgson, E. A. MacRae, and C. M. Triggs. 1989. Role of fruit firmness in the sensory evaluation of kiwifruit (*Actinidia deliciosa* cv Hayward). J. Sci. Food Agr. 47:417–433.

Strik, B. 2002. Aronia and hardy kiwifruit production. http://www.wwha.wsu.edu/proceedings/Kiwifruit%20and%20Aronia%20WWHA%202002.htm.

Strik, B., and H. Cahn. 2000. Kiwifruit cultivars. http://berrygrape.oregonstate.edu/fruitgrowing/berrycrops/kiwi/kiwicult.htm

Suezawa, K. 1989. Morphological variation of interspecies hybrid of *Actinidia*. Bul. Kagawa Agr. Expt. Sta. 40:36–42.

Sun, H.-M., and R.-H. Huang. 1994. *Actinidia hubeiensis*—a new species of *Actinidia*. J. Wuhan Bot. Res. 12:321–323.

Sun, Y.-W., J.-F. Wang, and Z.-Z. Qu. 1981. History of cultivation and dissemination of mihoutao. p. 1–6. In: Z.-Z. Qu (ed.), Mihoutaode zaipei he liyong. Nongye Chubanshe, Beijing.

Swaminathan, M. S. 1970. The significance of polyploidy in the origin of species and species groups. p. 87–96. In: O. H. Frankel and E. Bennett (eds.), Genetic resources in plants—their exploration and conservation. Blackwell, Oxford.

Tanaka, H., Y. Shoyama, Y. Sasaki, and Y. Sashida. 1997. Micropropagation of *Actinidia polygama* from fruit galls. Plant Cell, Tissue Organ Culture 48:135–137.

Tang, S.-X., and S.-F. Jiang. 1995. Detection and observation on the bud mutation of *Actinidia chinensis* Planch. Acta Hort. 403:71–73.

Testolin, R. 2001. Jintao®: nuova varietà di actinidia a polpa gialla. Inf. Agrar. 57(36):57–58.

Testolin, R. 2005. Quale spazio produttivo e commerciale per le nuove varietà di actinidia? Riv. Frutticolt. Ortofloricolt. 67(9):18, 20–23.

Testolin, R., and G. Cipriani. 1997. Paternal inheritance of chloroplast DNA and maternal inheritance of mitochondrial DNA in the genus *Actinidia*. Theor. Appl. Genet. 94: 897–903.

Testolin, R., G. Cipriani, and G. Costa. 1994. Genetic solutions to kiwifruit culture in Italy. p. 85–96. In: R. Monet (ed.), Production du kiwi (*Actinidia deliciosa*) en Europe. Redements, qualité et aspects economiques. VI/4126/94-FR. Commission Européenne, Brussels.

Testolin, R., G. Cipriani, and G. Costa. 1995a. Sex segregation ratio and gender expression in the genus *Actinidia*. Sex. Plant Reprod. 8:129–132.

Testolin, R., G. Cipriani, and G. Costa. 1995b. Estimate of variance components and heritability of characters in kiwifruit. Acta Hort. 403:182–188.

Testolin, R., G. Cipriani, and G. Costa. 1999a. Selezioni avanzate di actinidia e miglioramento genetico in Italia. Riv. Frutticolt. Ortofloricolt. 61(12):14–17.

Testolin, R., G. Cipriani, and R. Messina. 1999b. Sex control in *Actinidia* is monofactorial and remains so in polyploids. p. 173–181. In: C. C. Ainsworth (ed.), Sex determination in plants. Biosis Scientific Publishers, Oxford.

Testolin, R., G. Cipriani, A. R. Ferguson, and R. C. Gardner. 1997. Molecular approaches to systematics of *Actinidia*. Acta Hort. 444:97–102.

Testolin, R., G. Cipriani, L. Gottardo, and G. Costa. 1995c. Valutazione de selezioni maschili di actinidia come impollinatori per la cv. "Hayward". Riv. Frutticolt. Ortofloricolt. 57(4):63–68.

Testolin, R., and A. R. Ferguson. 1997. Isozyme polymorphism in the genus *Actinidia* and the origin of the kiwifruit genome. Syst. Bot. 22:685–700.

Testolin, R., W.-G. Huang, and G. Cipriani. 1999c. Towards a linkage map in kiwifruit (*Actinidia chinensis* Planch.) based on microsatellites and saturated with AFLP markers. Acta Hort. 498:79–84.

Testolin, R., W. G. Huang, O. Lain, R. Messina, A. Vecchione, and G. Cipriani. 2001. A kiwifruit (*Actinidia* spp.) linkage map based on microsatellites and integrated with AFLP markers. Theor. Appl. Genet. 103:30–36.

Testolin, R., R. Messina, O. Lain, and G. Cipriani. 2004. A natural sex mutant in kiwifruit (*Actinidia deliciosa*). New Zealand J. Crop Hort. Sci. 32:179–183.

Titlyanov, A. A. 1963. The biochemical composition and economic use of *Actinidia*. 5 pp. In: Physiology of the nutrition, growth, and resistance of plants in Siberia and the Far East. Proc. 1st Conf. of Physiologists and Biochemists on Plants of Siberia and the Far East, Irkatsk, 1960. USSR Academy of Sciences. Moscow.

UPOV (International Union for the Protection of New Varieties of Plants) 2001. TG/98/6. Guidelines for the conduct of tests for distinctness, uniformity and stability. *Actinidia* Lindl. UPOV, Geneva.

USDA (United States Department of Agriculture) Bureau of Plant Industry. 1907a. P.I. No. 11629, P.I. No. 11630. *Actinidia* sp., p. 63. Seeds and plants imported during the period from December, 1903, to December, 1905. Invent. 11 (Bul. 97). Government Printing Office, Washington, DC.

USDA (United States Department of Agriculture) Bureau of Plant Industry. 1907b. P. I. No.18535. *Actinidia chinensis*, p. 90. Seeds and plants imported during the period from December, 1905, to July, 1906. Invent. 12 (Bul.106). Government Printing Office, Washington, DC.

USDA (United States Department of Agriculture) Bureau of Plant Industry. 1909. P. I. No. 21781. *Actinidia chinensis* Planch., p. 14. Seeds and plants imported during the period from January 1 to March 31, 1908. Invent. 14 (Bul. 137). Government Printing Office, Washington, DC.

USDA (United States Department of Agriculture) Bureau of Plant Industry. [1910?]. *Actinidia chinensis*, yang tau vine. Bul. Foreign Plant Introductions 50, October 16 to 31, 1910. Unnumbered plate.

USDA (United States Department of Agriculture) Bureau of Plant Industry. 1911. P. I. No. 26904. *Actinidia* sp., p. 46. Seeds and plants imported during the period from January 1 to March 31, 1910. Invent. 22 (Bul. No. 207). Government Printing Office, Washington, DC.

USDA (United States Department of Agriculture) Bureau of Plant Industry. 1915a. P. I. No. 35133. *Actinidia chinensis* Planchon, p. 45. Inventory of seeds and plants imported by the Office of Foreign Seed and Plant Introduction during the period from January 1 to March 31, 1913. No. 34. Government Printing Office, Washington, DC.

USDA (United States Department of Agriculture) Bureau of Plant Industry. [1915b?]. The Yang Taw vine (*Actinidia chinensis*) bearing a single immature fruit; the first to be produced in America. Bul. Foreign Plant Introductions 111–112, July–August 1915. Unnumbered plate.

USDA (United States Department of Agriculture) Bureau of Plant Industry. 1918. P. I. No. 41401. *Actinidia chinensis* Planch., p. 24. Inventory of seeds and plants imported by the Office of Foreign Seed and Plant Introduction during the period from October 1 to December 31, 1915. No. 45. Government Printing Office, Washington, DC.

USDA (United States Department of Agriculture) Bureau of Plant Industry. 1922. P. I. No. 45946. *Actinidia chinensis* Planch., p. 46. Inventory of seeds and plants imported by the Office of Foreign Seed and Plant Introduction during the period from January 1 to March 31, 1918. No. 54. Government Printing Office, Washington, DC.

Valmori, I. 1991. Nuove varietà in frutticoltura. Edizioni Agricole, Bologna.

Veitch, J. H. 1904. Recently introduced trees and shrubs, &c. from Central China. J. Roy. Hort. Soc. 28:57–70.

Veitch, J. H. 1906. Hortus Veitchii. James Veitch & Sons, Ltd, Chelsea, [London].

Vilmorin, M. L. de, and D. Bois. 1904. Fruticetum Vilmorianum. Catalogus Primarius. Catalogue des arbustes existant en 1904 dans la collection de M. Maurice Levêque de Vilmorin avec la description d'espèces nouvelles et d'introduction récente. Libraire Agricole, Paris.

Vorobiev, D. P. 1939. Review of far-eastern species of genus *Actinidia*. Tr. Gorn. Stant. Dal'nev. Fil. Akad. Nauk. SSSR Vlad. 3:5–38.

Walker, E. H. 1976. Flora of Okinawa and the Southern Ryuku Islands. Smithsonian Inst., Washington, DC.

Walker, S., and J. Prescott. 2003. Psychophysical properties of mechanical oral irritation. J. Sens. Studies 18:325–346.

Wang, M., M. Li, and A. Meng. 2003. Selection of a new red-fleshed kiwifruit cultivar 'Hongyang'. Acta Hort. 610:115–117.

Wang, M.-Z., X.-D. Li, Z.-S. Yu, M.-Z. Li, and S.-S. Song. 2005. Breeding report on the red-fleshed cultivar 'Hongmei'. China Fruits 2005 (4):7–9.

Wang, S., Z. Jiang, H. Huang, Z. Zhang, and J. Ke. 2003. Conservation and utilization of germplasm resources of the genus *Actinidia*. Acta Hort. 610:365–371.

Wang, S.-M., R.-H. Huang, X.-W. Wu, and K. Ning. 1994. Studies on *Actinidia* breeding by species hybridization. J. Fruit Sci. 11:23–26.

Wang, S.-M., X.-W. Wu, R.-H. Huang, Z.-T. Xiong, and S.-Q. Ke. 1989. Preliminary report on fluctuation of interspecific crosses of Chinese gooseberry. J. Wuhan Bot. Res. 7: 399–402.

Wang, Z.-Y., C.-H. Zhong, and F.-W. Bu. 2004. A new red-fleshed kiwifruit cultivar 'Chuhong'. Agr. Sci. Technol. (China) 5(4):23–24 + back cover.

Warrington, I. J. 1990. Areas and trends of kiwifruit production in New Zealand and around the world. p. 511–525. In: I. J. Warrington and G. C. Weston (eds.), Kiwifruit: science and management. Ray Richards Publ. and New Zealand Soc. Hort. Sci., Auckland.

Watanabe, K., S. Hirota, and B. Takahashi. 1986. Determination of chlorophyll and carotenoid pigments in kiwifruit. Nip. Shok. Kogyo Gak. 33:616–620.

Watanabe, K., and B. Takahashi. 1984. Flower bud differentiation and development of kiwi (*Actinidia chinensis* Planch.). J. Japan. Soc. Hort. Sci. 53:259–264.

Watanabe, K., and B. Takahashi. 1998. Determination of soluble and insoluble oxalate contents in kiwifruit (*Actinidia deliciosa*) and related species. J. Japan. Soc. Hort Sci. 67: 299–305.

Watanabe, K., B. Takahashi, and K. Shirato. 1990. Chromosome numbers in kiwifruit (*Actinidia deliciosa*) and related species. J. Japan. Soc. Hort. Sci. 58:835–840.

Webby, J. 2004. New Zealand Kiwifruit J. 100 Year Centennial Edition.

Webby, R. F., R. D. Wilson, and A. R. Ferguson. 1994. Leaf flavonoids of *Actinidia*. Biochem. Syst. Ecol. 22:277–286.

Weising, K., R. W. M. Fung, D. J. Keeling, R. G. Atkinson, and R. C. Gardner. 1996. Characterisation of microsatellites from *Actinidia chinensis*. Mol. Breed. 2:117–131.

White, A., and R. Beatson. 1993. Evaluation of a new kiwifruit hybrid. p. 161–163. In: Proc. Australasian Postharvest Conf., Gatton College, Queensland, 20–24 September 1993.

White, A., H. N. De Silva, C. Requejo-Tapia, and F. R. Harker. 2005. Evaluation of softening characteristics of fruit from 14 species of *Actinidia*. Postharvest Biol. Technol. 35:143–151.

White, J. 1986a. Ontogeny and morphology of ovarian and fruit hairs in kiwifruit. New Zealand J. Bot. 24:403–414.

White, J. 1986b. Morphology of the fruit hairs in cultivars of *Actinidia deliciosa* var. *deliciosa*, *Actinidia eriantha* and *Actinidia rufa*. New Zealand J. Bot. 24:415–423.

White, J. 1990. Pollen development in *Actinidia deliciosa* var. *deliciosa*: histochemistry of the microspore mother cell walls. Ann. Bot. (Lond.) 65:231–239.

Williams, M. H., L. M. Boyd, M. A. McNeilage, E. A. MacRae, A. R. Ferguson, R. A. Beatson, and P. J. Martin. 2003. Development and commercialization of 'baby kiwi' (*Actinidia arguta* Planch.). Acta Hort. 610:81–86.

Wilson, E. H. 1909. Plant collecting in China. Gardeners' Chronicle 3rd Series, 45:24–25.

Wilson, E. H. 1913: A naturalist in western China with vasculum, camera and gun. Methuen, London.

Wismer, W. V., F. R. Harker, F. A. Gunson, K. L. Rossiter, K. Lau, A. G. Seal, R. G. Lowe, and R. Beatson. 2005. Identifying flavour targets for fruit breeding: a kiwifruit example. Euphytica 141:93–104.

Wong, M. 1969. Contribution à l'histoire de la matière végétale chinoise. J. Agr. Trop. Bot. Appl. 16:158–214, 284–334.

Wong, M. 1970. Contribution à l'histoire de la matière végétale chinoise. J. Agr. Trop. Bot. Appl. 17:92–140, 368–401.

Wu, B.-L., and X.-D. Li. 1993. 'Hongyang'—a red-fleshed, top quality and good storing kiwifruit cultivar. China Fruits 1993 (4):15, 27.

Wu, X.-W., R.-H. Huang, S.-R. Hong, and S.-M. Wang. 1987. Exploitation and utilization of *Actinidia* resources in Hubei. J. Wuhan Bot. Res. 5:172–184.

Xiao, X.-G. 1999. Progress of *Actinidia* selection and breeding in China. Acta Hort. 498:25–35.

Xin, F.-W., F. Cheng, Z.-X. Li, and W.-X. Pan. 1990. Survey on germplasm resource of *Actinidia* in Guangdong province. Guangdong Agr. Sci. 33(1):18–22.

Xin, S.-Z. 1983. Study of fruit tree history in China. Agriculture Press, Beijing.

Xiong, Z.-T. 1990. Observation on the morphology and meiosis of interspecies hybrid triploid in *Actinidia*. Bul. Bot. Res. 10:99–103.

Xiong, Z.-T. 1991. Studies on the phylogenetic relationship between *Actinidia chinensis* and *A. deliciosa* using cladistic analysis. Guihaia 11:36–39.

Xiong, Z.-T. 1992. Chromosome studies on cultivated Chinese gooseberry. Guihaia 12:79–82.

Xiong, Z.-T., and R.-H. Huang. 1988. Chromosome numbers of 10 species and 3 varieties in *Actinidia* Lindl. Acta. Phytotaxon. Sin. 26:245–247 + 2 plates.

Xiong, Z.-T., R.-H. Huang, and X.-W. Wu. 1985. Observations on the chromosome numbers of 4 species in *Actinidia*. J. Wuhan Bot. Res. 3:219–223.

Xiong, Z.-T., R.-H. Huang, and X.-W. Wu. 1998. Chromosome numbers of several strains of *Actinidia chinensis* var. *chinensis*. J. Wuhan Bot. Res. 16:302–304.

Xiong, Z.-T., R.-H. Huang, P. Yuan, and X.-W. Wu. 1993. Cytological observations on the meiosis of PMC and pollen development of tetraploid in *Actinidia chinensis*. Guihaia 13:139–142.

Xu, X.-B., X.-H. Yao, and H. Chen. 2003. Application of modern biotechnology on kiwifruit. Acta Hort. 610:525–531.

Yan, G.-J. 1996. Cytogenetic and molecular studies of *Actinidia* genomes. Ph.D. thesis, Univ. of Auckland.

Yan, G.-J., R. G. Atkinson, A. R. Ferguson, M. A. McNeilage, and B. G. Murray. 1997a. In situ hybridization in *Actinidia* using repeat DNA and genomic probes. Theor. Appl. Genet. 94:507–513.

Yan, G.-J., A. R. Ferguson, and M. A. McNeilage. 1994. Ploidy races in *Actinidia chinensis*. Euphytica 78:175–183.

Yan, G.-J., A. R. Ferguson, M. A. McNeilage, and B. G. Murray. 1997b. Numerically unreduced (2*n*) gametes and sexual polyploidization in *Actinidia*. Euphytica 96:267–272.

Yan, G., J. Yao, A. R. Ferguson, M. A. McNeilage, A. G. Seal, and B. G. Murray. 1997c. New reports of chromosome numbers in *Actinidia* (Actinidiaceae). New Zealand J. Bot. 35:181–186.

Yan, J.-Y. 1981. Histoire d'*Actinidia chinensis* Planch. et conditions actuelles de sa production à l'étranger. J. Agr. Trad. Bot. Appl. 28:281–290.

Yao, J.-L., and Z.-X. Cui. 1988. Observations on the chromosome numbers of species of *Actinidia*. J. Fruit Sci. 5:24, 25.

Yao, X.-H., X.-B. Xu, P.-X. Gao, Z.-Z. Li, and H.-W. Huang. 2005. The geographical distribution and flora of *Actinidia* in Jiangxi province. J. Wuhan Bot. Res. 23:257–261.

Yerex, D., and W. Haines. 1983. The kiwifruit story. Agricultural Publ. Assoc., Masterton.

Yin, W.-F., and X. Li. 1982. A study of the variation in the vitamin C content of the fruits of *Actinidia chinensis* Planch. Acta Hort. Sin. 9(2):31–35.

Young, H., and V. J. Paterson 1990. The flavour of exotic fruit. p. 281–326. In: I. D. Morton and A. J. MacLeod (eds.), Food flavours. Part C. The flavour of fruits. Elsevier, Amsterdam.

Yu, L.-L. 1988. A new variety of *Actinidia valvata* Dunn. Guihaia 8:132.

Zambujo, C. V. 2003. Du nouveau . . . hors de France. Arb. Fruit. 568:32–33.

Zhang, J. 2000. Conservation strategies on species diversity of *Actinidia* in the 21st century. p. 90–94. In: H.-W. Huang (ed.), Advances in *Actinidia* research. Science Press, Beijing.

Zhang, J., and E. J. Beuzenberg. 1983. Chromosome numbers in two varieties of *Actinidia chinensis* Planch. New Zealand J. Bot. 21:353–355.

Zhang, J., J.-R. Wang, D.-R. Cai, and H.-X. An. 1983. Studies on the introduction and selection of Chinese gooseberries (*Actinidia chinensis* Planch.). Acta Hort. Sin. 10:93–98.

Zhang, Y.-J., Y.-Q. Qian, Q.-G. Cai, X.-J. Mu, X.-P. Wei, and Y.-L. Zhou. 1997. Somaclonal variation in chromosome number and nuclei number of regenerated plants from protoplasts of *Actinidia eriantha*. Acta Bot. Sin. 39:102–105 + 1 plate.

Zhang, Z.-H., S.-Y. Lu, S.-M. Wang, and H.-W. Huang. 2000. Current situation of endangered *Actinidia* species and countermeasure of *ex situ* conservation. p. 99–102. In: H.-W. Huang (ed.), Advances in *Actinidia* research. Science Press, Beijing.

Zhang, Z.-Y. 1983. A report on the chromosome numbers of two varieties of *Actinidia chinensis* Planch. Acta Phytotaxon. Sin. 21:161–163.

Zhao, Y.-L., and X.-P. Liu. 1996. Study on the geographical distribution and floristic characteristics of the genus *Actinidia* Lindl. from Hunan. Guihaia 16:9–16.

Zhao, S., M. Wang, G. Yang, L. Zhang, and J. Zhou. 2003. Fruit quality assessment of twelve introduced kiwifruit varieties planted in China. Acta Hort. 610:61–68.

Zhen, Y.-Q., Z.-Z. Li, H.-W. Huang, and Y. Wang. 2004. Molecular characterization of kiwifruit (*Actinidia*) cultivars and selections using SSR markers. J. Am. Soc. Hort. Sci. 129:374–382.

Zhu, D.-Y. 1982. The primary studies of the cell division and the chromosome numbers for germplasm resources of *Actinidia* in Henan Province. J. Henan. Agr. Coll. 1:45–58.

Zhu, D.-Y. 1990. Phenotypic and genotypic variation in kiwifruit (*Actinidia deliciosa* (A. Chev.) C.F.Liang et A.R.Ferguson) seedling populations. Ph.D. thesis, Massey Univ., Palmerston North.

Zhu, D.-Y., G. S. Lawes, and I. L. Gordon. 2002. Estimates of genetic variability and heritability for vegetative and reproductive characters of kiwifruit (*Actinidia deliciosa*). Euphytica 124:93–98.

Zhu, H.-Y. 1983. Zhonghua *mihoutao* zaipei. Shanghai Kexue Jishu Chubanshe, Shanghai.

Zhu, L., and S. Ding. 2003. Evaluation of the sport selected from *Actinidia deliciosa* cv. Hayward. Acta Hort. 610:109–114.

Zuccherelli, G. 1994. L'actinidia e i nuovi kiwi. Edagricole-Edizioni Agricole, Bologna.